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A Comparative Study of Innate Defensive Behavior in Trinidad Mantids (Orthoptera, Mantoidea).[1]

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(Plates I-X; Text-figures 1 & 2)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, British West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe. (Zoologica, 1952, Vol. 37, No. 13, pp. 157-184)]

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I. INTRODUCTION

ALTHOUGH mantids have often been studied as efficient predators, their remarkable specializations for escaping enemies have seldom been considered. The first description of a mantis display was written by Goureau who, in 1841, gave a lively account of the posturing of *Mantis religiosa* before a threatening hand, her wings erected and forelegs spread. It is a display typical of the best in the group, and this early account was a worthy pioneer study. However, it was also typical of the work of his successors, for while many striking "frightening" displays have been placed on record, the varied other and more usual means by which mantids escape their predators seem rarely to have been studied. Except for a few references to their concealing coloration and to resemblances to leaves and sticks, the subject has remained unexplored. Since in this one small group are found four out of the seven major types of defense which occur in the animal kingdom, the special interest of a comparative study is apparent.

In 1939 Varley gave an excellent résumé of the published references to display, evaluating the widely scattered descriptions from Europe, Africa, the Far East and the Americas, and apportioning them among the recognized subfamilies. Since then no further display descriptions seem to have appeared. However, two general references are important to the subject, namely, Cott (1940), who was quoted from manuscript by Varley, and Chopard (1950). The points of view of both authors in regard to the effectiveness of display, concealing coloration and mimicry, will be considered later.

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In his paper Varley remarked on the lack of a comparative and experimental study of mantis displays. The present paper is a preliminary contribution toward that end. Its purpose is to describe, analyze and compare innate defensive behavior patterns in a number of species of mantids as an example of behavior evolution in a restricted animal group. A particular effort has been made, apparently for the first time, to trace the postembryological beginnings and development of the defense patterns of the adults. The behavior has also been examined, to a limited extent, from the point of view of innate releasing mechanisms, as has been done by Lorenz, Tinbergen and their associates, who have worked almost altogether with vertebrates. (Tinbergen, 1948; Lorenz, 1950; and references). Evolutionary aspects are discussed, with suggestions concerning the origins of the elements.

In the present study, as with a somewhat similar comparative survey of certain salticid spiders (Crane, 1949), there were great advantages in working for several successive seasons in a tropical field laboratory. Thanks to its favorable location, fifteen species were available for comparison, all taken in the immediate vicinity. In addition, as is often the case with tropical invertebrates, young of all the common species occurred throughout the laboratory season, which extended for three years from January through June.

An annotated list of this same group of Trinidad mantids has already been published (Beebe, Crane & Hughes-Schrader, 1952). It includes references, notes on color in life and ecological data. Also included are keys and photographs for field recognition of this group of species. The photographs in the present paper are restricted to those illustrating defensive behavior or its possible derivations from elements in resting positions.

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Grateful appreciation also goes particularly to my co-workers in the Simla laboratory, Dr. William Beebe, Mr. Henry Fleming, Miss Ellen Ordway and Mr. John Cody. Their help ranged the full gamut of chores necessary in any study of ever-hungry mantids — the catching of mantids in the field and at night lights, the rearing or collecting of endless hundreds of *Drosophila*, grasshoppers and moths, and, especially, the perennial furnishing of much-needed encouragement and advice. The Text-figures and Plate X are the work of Mr. Cody.

II. Material and Methods

Fifteen species of mantids serve as the material on which this paper is based. An exact record of the number of specimens taken was kept only during 1952. On that year, from February to June, inclusive, 197 individuals were brought into the laboratory, not counting specimens hatched from oöthecae or first instar young taken in the field. Their distribution among the species and other data regarding material will be found in Beebe, Crane & Hughes-Schrader, 1952.

Mantids have been successfully collected, kept alive and reared for observation, experiment and even pleasure by so many people in so many countries that no special comment on techniques is needed. General remarks, along with pertinent recent references, are given in the paper mentioned above, p. 247.

In experimental work on innate behavior, the usual precautions were observed, following the general rules which were given in a similar work on salticids (Crane, 1948). Detailed discussion concerning the effects of the law of heterogeneous summation, etc., will be found in Tinbergen (1948) and Lorenz (1950). These are supremely relevant to any experimental work with mantid behavior. The following point only will be specially mentioned in this connection: adequate rest periods, the length of which is entirely dependent on the species, are particularly essential in this group, between experiments with the same individuals in the same series, except in cases where the cumulative effects of stimuli were being studied.

In order to rule out possible side effects from the appearance and motion of the observer, all results were checked at least twice with the observer completely hidden behind a black curtain, with one small slit for vision. In these cases, manipulation of the mantid and stimuli (lizard, pencil, etc.) were accomplished by sticks or long forceps covered with black tape. In eye blacking, Floquil paint was used, as in salticid spiders.

Some of the observations and experiments were made with the mantids in their own large, glass-sided terraria; others in the open laboratory; still others in a small room with large glass windows and black curtains, so that light could be restricted to a single direction; others were made in the even, natural lighting of the out-of-door insectaries. In the latter, both roof and sides are made of fine wire screening. One measures 12 × 18 feet in area and about 9 feet in height at the ridgepole; and the other measures 24 × 36 × 12 feet. Both are furnished with growing herbs, shrubs, small trees, epiphytes and vines, and include areas of open sunlight. In the larger cage especially, natural conditions are closely approximated.

The following terms used in the present paper require definition or comment:

The instars are numbered, as usual in this group, exclusive of the prelarval stage. For example, the "first instar" indicates the stage following the shedding of the whitish skin which is molted immediately upon emergence and which is left attached to the oötheca.

As usual in papers of this type, it seems impossible to avoid the use of a few terms which can be accused of having anthropomorphic significance. No such significance is of course intended. Such terms are used as a practical convenience to describe situations which otherwise would require unwieldy circumlocutions, or, sometimes, the use of recent words with definitions as yet unstabilized on the two sides of the Atlantic. An example is the use in this paper of the phrase "apparent awareness of threat." Still using ordinary English words, without recourse to recent vocabulary, it may be more precisely phrased as follows: "Indication to the experienced observer, through the mantid's position or behavior, that the insect has received, through one or more sense organs, a stimulus which may lead to defensive behavior." The short-hand phrase will, however, be used without apology.

In addition the following words and terms will be used freely in the restricted senses given:

By "defensive behavior" is understood any behavior pattern which has been observed to occur in the face of actual danger from a natural predator, and which has been found by observation and experiment to lead in at least some cases to the survival of the mantid.

"Threat" is used to cover any object or part of an object, animate or inanimate, which elicits, or might be expected to elicit, any element of defensive behavior.

"Rearing" is applied to the common mantid practice of elevating the prothorax; "flexing" and "flexed" to describe the bending of the various segments of the forelegs against one another; "freezing" to cover the semi-rigid motionlessness, accompanied by apparent awareness of threat, which is such an important element in mantid defense. "Kataplexy," on the other hand, is used in the sense of perfect quiescence, the insect lying on its side and giving no apparent response to handling or touching; normal motion can usually be restored, as in many insects, by stimulation of the tarsi. "Stick formation" and "stick position" are used to cover the entire complex of motions going into the enhancement of the structural resemblance of some mantids to twigs. By "grooming" is meant the cleaning motions, termed "comfort motions" by some behaviorists, made in mantids by the jaws and forelegs over various parts of the body.

"Startle display," or simply "display," covers the type of behavior in which tegmina and wings are elevated and special associated motions made in the face of a potential threat. The more usual terms "frightening" or "intimidating display" seem too strong to apply in most of the current instances.

Finally, "teasing" is used for the gentle prodding or near-prodding of a mantid from the front with fingers, pencil, forceps, etc.

Since the behavior of only a single species of each genus was studied, the various forms are designated in the body of the text merely by their generic names. None of the observations, of course, is intended to apply to any other species, which must await similar study.

It seemed desirable to preface the specific accounts of defensive behavior with descriptions of rest positions and locomotion, because of their importance in both the practice and derivation of defense.

Attention may be here directed to the photographs of dried examples of this same group of species in Beebe, Crane & Hughes-Schrader (1952), since they give a particularly good idea of the basic structural diversity of the group and supplement the pictures of living mantids in the present paper.

A special word will be said here concerning the lizards and other animals used in inducing display in mantids. Three sizes of lizards were kept on hand: *Polychrus marmoratus,* about 350 to 450 mm overall, of which more than two-thirds is tail length; medium-sized *Gonotodes humeralis* (Guich.), about 75 mm in total length; and small *Gonotodes vittatus* (Lich.), ranging from 25 to 35 mm. In addition, a snake, *Leptodeira a. annulata* (L.), 320 mm long, was used, as well as a capuchin monkey and an assortment of large insects, including carnivorous grasshoppers and katydids. The *Polychrus* was by far the most convenient stimulus, since this genus always becomes exceedingly tame within a few days, is phlegmatic and slow-moving in disposition, can be manipulated before a mantid with relative ease and, provided it is well fed immediately before an experimental session, is not apt to snap up one's rarest specimens.

The photographs were all made with a Leica camera, with reflex finder, bellows extension and the front element of the 135 mm lens. Some were made by Leitz flash at 1/100 or 1/200 sec., and others at 1/5000 sec., with the focal plane shutter set at 1/20 sec. and the Revelec speedlamp used in subdued light.

III. Elements of Defense Mechanisms in Mantids

In the Mantoidea studied at Simla, protection against predators is obtained by four general means. The first employs a resemblance to the surroundings, either general or specific. This includes similarities in both structure, including coloration, and in behavior, the latter consisting basically of immobility. The second means of defense is by active escape through a variety of means. The third makes use of a sudden display in which appendages are extended while colors and striking markings, usually hidden, are revealed; one invariable effect of the display is to make the insect appear larger than usual. The fourth and final method is by actual attack, using as weapons the spiny forelegs and sometimes following through by biting with the mandibles. Two, three, or even all four general methods are combined in the defense behavior pattern of all the Trinidad species after they have reached the adult stage.

Since this group of mantids fortunately represents genera widely scattered through the family, the distribution and combination of these methods, their variations and similarities and their correlation with structural characteristics, have proved to be of particular interest.

These major types of behavior – immobility, escape, a "bluffing" display and attack – may be counted as four out of six or seven major types of defense activities found in the animal kingdom.

A fifth type, which seems of great enough importance to be a major classification, is withdrawal into a well-protected position. This may be a self-made fortress, as in anemones, snails, turtles or porcupines, or a physically strong niche of the environment. In the latter category belong the crannies of multitudes of occasionally retiring creatures, from naked mollusks and small reef crabs, each within reach of a crack in the coral, to tree-frogs in airplants and gophers near holes. For this almost universal type of defense the mantids have no apparent counterpart. Incorrigibly photophilic, they never lurk behind bark, burrow in rotten wood or fasten leaves into a shelter, although they could conceivably master each of these activities with very little further evolution in their physical equipment. All of their concealment is superficial and make-believe.

As the sixth major division may be counted the property of inedibility, or at least of unpalatability. It depends for success, of course, chiefly on the learning ability of vertebrate predators. However, both mantids and carnivorous grasshoppers in our laboratory have rejected aposematic butterflies and moths after their capture but before the lepidopterans were injured. On the other hand, none of our brightly colored common species of mantids was rejected by either monkeys or lizards. Although none of our rare species was tested for inedibility, none of them was brightly colored; it therefore seems probable that this aposematic characteristic does not occur in these species. Neither have I found any record in the literature of a distasteful mantid. Hence, as far as present knowledge goes, all mantis display is pure bluff except when some small animal is vulnerable enough to be hurt by an actual mantid attack.

A related subdivision, which is not known to occur in mantids but which is present in some Orthoptera and many other animals, is the exuding of a sticky, bad-smelling, irritating or otherwise repellant substance. This could be regarded either as a subdivision of the aposematic property or of display. Still another type of defense which is superficially similar is the active injection of poison, such as through bee-stings, through the fangs of snakes or through the spur of the platypus. It seems clear, however, that in these latter cases the poison is a reinforcement of actual physical attack and should be considered a subdivision of that category.

Finally, a possible seventh major type of defense which defies location in any one preceding group is the exudation of a presumably confusing "smoke-screen," as found in cephalopods and deep-sea shrimp. Here again is a system unknown in mantids.

Nevertheless, however animal defense is classified, this one small group of orthopterans exhibits a large percentage of all known methods of escaping natural foes.

The following remarks on the four types of mantid defense may serve as an orientation preceding the systematic account of defense and its development in the various species.

1. *Protective Resemblance.*– This is a uni-

versally distributed basic means of mantid defense. It ranges in structure from the general inconspicuousness of brown or green coloration to the almost fantastic mimicry of some species to sticks or leaves. This is brought about by the widest possible range of shapes of thorax, abdomen and leg segments. In behavior, the correlated specializations extend from simple immobility to a convincing trembling, as though breeze-blown, in dead-leaf insects, and a leaf-like fluttering in flight. There is also correlated extension or folding of various appendages, which heighten the resemblance. The best examples are the stick mantids, which stretch the forelegs straight ahead and hold them rigidly apposed.

2. *Active Escape.*— This method is also characteristic of all mantids under certain conditions. Associated with it are degrees of dexterity in rapid walking or climbing, strength of flight, aptitude for jumping, ability to dodge and ability to drop instantly from a perch. A form of kataplexy, a non-rigid motionlessness in an unnatural position, occurs occasionally in mantids and may be included in the category of escape. Color is not concerned in escape except in the indirect sense leading to inconspicuousness in flight, or, perhaps, "flash" or "dazzle" coloration may also occasionally be involved.

3. *Startle Display.*— This method of defense occurs infrequently and in relatively few species. It requires no obvious morphological specializations, with the exception of bright color or contrasting markings. Stridulatory apparatus, which has been reported in Bornean and African species (Shelford, 1903; Carpenter, 1921), has not been found in Trinidad species. Specialized display coloration, invisible or at least inconspicuous when the mantis is not displaying, includes bright mandibles and foretarsi, spotted foretibiae, a black bar between forecoxae on sternum, eye-like spots on tegmina and brilliantly colored or glossy hindwings and dorsum. The special motions associated with display may be summarized as follows: cocking of antennae forward or backward; opening and shutting of mouthparts; extension to sides or overhead of forelegs, or special twisting in flexing to show tibial markings; elevation of prothorax, tegmina and wings; vibration of wings; elevation, pulsation, lateral twisting and tilting of abdomen; swaying, sidling or turning as necessary to show to best advantage the expanse of colored surfaces listed above. Most of these separate motions are combined into a full display, and in spite of distinct specific differences the display of even widely separated genera are basically similar.

4. *Aggressive Attack.*— In the relatively few forms which resort to actual counter-attack, the same armature of the foreleg is used as in catching prey. In defense, however, instead of grasping the enemy, the usual procedure is merely a lightning-swift rake with the spines of femora and tibiae, which are extended, boxer-like, from their tightly flexed position against the prothorax. The latter segment at these times is always strongly reared. Actual biting occurs rarely, when the mantis is seized and at the end of its resources.

In the systematic account that follows, a paragraph is given in each case concerning the normal rest position and habits of locomotion, since the defensive behavior often depends upon or proceeds from these basic patterns.

Releasing mechanisms will be considered only casually in the systematic section, amplification being reserved for the final pages. Here it may be said that the releasers for defensive behavior are undoubtedly primarily visual, and depend largely on perception of a moving object of appropriate size. A secondary releaser in some species is probably chemical, although not chemotactic. A third factor, governing some types of defense response, may to be kinaesthetic, since in a number of species display is usually induced only in a fairly enclosed space, such as a terrarium.

Discussion of the effectiveness of defense and evolutionary aspects will also be reserved for the sections following the systematic account.

1. MANTOIDA sp.

(Plate I, Figure 1)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 247, Pl. I, Fig. 1.

Rest Position and Locomotion.—(Male only). Rest position usually hanging from underside of perch, with all six legs used in grasping. Tip of abdomen, however, is held closer to perch than head. Except when the insect has been completely immobile and absolutely undisturbed for many minutes, the antennae are kept in constant vibration, held forward, often close together. It was seen to sway only once. In locomotion it is extremely active, running rapidly, in short spurts, the body held close to the ground. Even when completely undisturbed the insect takes to flight freely and very swiftly. Although it is a capable jumper, the wings are often used in short jumps, either vertical or horizontal, and even in the restricted confines of a terrarium the eye can scarcely follow its flight. In fact, the general impression of this insect in flight is not only extremely unmantis-like but even reminiscent of a wasp. In view of its unspecialized mantine structure, this behavior is of exceptional interest.

Defensive Mechanisms.—(Male only). Because of the rarity of this species no tests were made for defensive behavior either with living enemies or outside the confines of the terrarium. The first response to a sharp knock on the screen to which it is clinging is a very slight rearing, followed by freezing, although the antennae continue to vibrate. Pursuit resulted in expert dodging and sometimes fluttering downward. Often it dodged straight backward, away from the disturbance, before almost instantaneously taking to the wing. In flight it dodged back and forth around the terrarium with bewildering dexterity, sometimes for more than a minute before coming to rest. Renewed disturbance brought renewed flight up to four times in succession, the insect by then being exhausted. There never was any trace of display or attack. Thus, in the present incomplete state of our knowledge, the primary type of defense may be said to be freezing, without stick formation, and the second type escape. In the latter, flight certainly plays a far larger part than in any other Trinidad mantis.

2. LITURGOUSA sp.

(Plate I, Figures 2, 3)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 247, Pl. I, Fig. 2.

Rest Position and Locomotion.— In appearance and motions, *Liturgousa* is, next to *Mantoida,* the least typical mantis of the Arima Valley. It skitters along, always on all six legs, the body held close to a tree trunk, in a fashion reminiscent of the littoral isopod *Ligia.* Even when resting, with the first legs flexed and clear of the ground, the prothorax and head are scarcely bent upward.

Young *Liturgousa,* measuring only 4.3 mm in length and presumably of the first or second instar, are very similar to adults in both general coloration and behavior. Rarely, however, the abdomen may be turned upward during rest; this is never true of larger nymphs or of adults. At rest they rear quite high up, the forelegs flexed, and the whole body in walking is held higher relatively than in adults. Unlike adults, nymphs of all ages do not always use the forelegs in running, jumps are occasionally made in simple exploring and slight swaying occurs in the pauses during exploration. The antennae are never vibrated, although they are more active than in the adult. When the young were stalking prey at a few millimeters' distance, the following motions were observed: both forelegs were extended obliquely forward, diverging, and jerked inward as they were reflexed. The motion may have something in common with the jerking of the parallel-held forelegs in *Promiopteryx* and similar behavior in exploration in *Thesprotia* and *Tithrone.*

Defensive Mechanisms.—This species depends primarily on immobility, combined with its cryptic coloration; the secondary line of defense is active escape.

The coloration bears a most effective resemblance to lichenous bark. Associated with it in effect is the dorso-ventrally flattened form of the body and the exaggerated compression of the second and third legs, with the anterior surfaces turned ventrally.

When threatened by nearby motion — whether by a natural enemy such as lizard or monkey, or by a pencil or human hand — the insect usually remains quite immovable or imperceptibly flattens even more closely against the bark. When actually touched or teased, either dorsally or from the front, it seeks to escape chiefly by dodging, skittering and slithering rapidly around the trunk, sometimes spiralling upwards; it is frequently difficult to catch. It can jump capably when pressed. As a last resort it takes to flight, but the dull wings are weak and scarcely do more than break its fall as it flutters to the ground. I have never seen a *Liturgousa* fly upward. A single female, when continuously teased from the front for more than a minute in a small aquarium, finally paused and reared slightly up, the forelegs folded. She did not strike, however, and this is the only time in numerous tests with more than 20 adult individuals in which I have seen this usually typical mantis behavior.

When individuals fall during teasing, or are gently dropped only an inch or two on their backs, reflex immobility usually occurs for a few minutes, the pale underparts being then very conspicuous.

The following general elements of mantid defensive behavior have never been seen in any form: stick position; lateral spreading of forelegs; tegmina and wing elevation; abdominal elevation or twisting; swaying, teetering or quivering. When the insect is teased the antennae are active, but there is no vibration or bending to front or rear.

Post-embryological Development of Defensive Behavior.— In defense the young are surprisingly similar to the adult in escape behavior, being excellent runners, jumpers and dodgers; they cling tightly to their substratum when shaken. However, unlike adults, they do not become immobile when first threatened.

3. Promiopteryx granadensis (Saussure)
(Plate I, Figures 4, 5)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 248, Pl. II, Figs. 6, 7; Pl. VIII, Fig. 28.

Resting Position and Locomotion.— This little brown mantis appears as a characteristic, if unspecialized, member of its group. Its preferred resting position is upsidedown on a vertical small twig, or more rarely a blade of grass, the head and prothorax often reared and the forelegs typically flexed. However, equally frequently, it rests with all six legs gripping its perch, the body forming an unbroken horizontal line; it does not, however, during rest, flatten itself against the twig. It is an excellent jumper, in ordinary locomotion, and the males are strong fliers, taking freely to wing even when not pursued; almost always they take off obliquely upward and are skillful at landing on the undersides of twigs or leaves, often many feet away.

Apparently of an exploratory, possibly sensory, rather than a defensive nature are the following motions. They occur in both sexes and all ages, even in the first instar: the forelegs are extended, parallel, with tibia and tarsi only flexed, first obliquely to the right and then without a pause to the left, with a vibratory, jerky motion. They are never held straight in front as in *Musonia, Catamusonia, Thesprotia* and *Angela,* or obliquely divergent as in *Liturgousa,* and are never held motionless when extended. Usually, the forepart of the body sways gently from side to side between series.

Often prothoracic swaying, with turned head, precedes jumping and always occurs before a leap for prey; it is very likely connected with vision; it is at least followed by walking if not by jumping in most cases. Antennae are usually held straight forward in exploring; they are not vibrated.

The general motions of the young are similar to those of the adults except that jumping is more common than in the larger, heavier insects. During the first instar, jumps up to six times the insect's length may occur on a flat surface.

Defensive Mechanisms.—The primary defense is active escape, the secondary, immobility combined with generalized concealing coloration.

This little dull mantis does not seem to depend much on its inconspicuous, brown coloration for concealment. The approach of either a natural enemy or artificial stimulus sends it running, dodging, jumping with excellent aim, or in the case of males, flying away with speed and skill. Often the first response is to run directly toward the threat and either climb on it or by-pass it; only rarely does it turn tail. When directly teased from the front, in or out of a container, or when cornered, it stops and rears the prothorax slightly up, the forelegs flexed. However, in its own environment, when first aware of the threat but not directly teased, the females and young may become immobile but alert, following the progress of the threat with turning heads, the forelegs flexed but the prothorax not reared. After a few minutes they may suddenly drop to the ground, sliding first imperceptibly around to the lower side of a twig or grass blade, and run away. More rarely they stay for a few minutes where they have dropped, motionless but alert, the head turned upward and toward the original source of danger.

The following elements of mantis behavior are not present in *Promiopteryx:* antennal vibration; jaw extension; stick position of forelegs; spreading of forelegs laterally; striking with forelegs; elevation of wings; elevation, twisting or quivering of abdomen.

Post-embryological Development of Defense Mechanisms.— Just as the typical "exploring" jerks of the forelegs are fully developed even in the first instar, so is the general defensive behavior similar to that of the adult. The chief differences are the slower awareness, or even lack of apparent awareness, of a suitable-sized moving object as a possible danger. When confronted with a small, moving lizard, which subsequently ate a number of these mantids in the first instar, several individuals at different times paid no apparent attention, continuing grooming and random motions of all kinds, in any direction, until eaten or bypassed. However, they can and do dodge at this age with moderate skill and can jump up to six times their own length, although they do so but rarely.

When they climb onto the threat, as seems in older examples to happen as a definite part of the defense, the movement seems merely an extension of the random motions. Immovability in the face of a threat was never seen. By the second instar, however, all of the technique of the adult has appeared except that, as in ordinary locomotion, jumping plays a relatively larger part, the antennae are often laid back during freezing and, of course, flight does not exist.

A 6 mm young, when tested with lizards up to 75 mm in total length, gave all of the appropriate responses; with the large, 430 mm *Polychrus,* however, the responses were imperfect: there was some immobility but no subsequent, sustained dodging, and exploring motions were at times continued actually under the lizard's snout without apparent awareness.

4. MUSONIA SURINAMA (Saussure)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 249, Pl. II, Figs. 8, 9; Pl. VIII, Fig. 30.

Rest Position and Locomotion.— Rest position usually hanging from underside of perch, forelegs flexed, prothorax scarcely reared. Does not sway in ordinary walking and climbing about cage. Little or no jumping.

Defensive Mechanisms.— General types: primary, immobility with stick formation; secondary, escape.

Single male, tested only in terrarium because of rarity: exceedingly similar to *Thesprotia* (p. 266). Goes into complete stick formation readily at the sudden pass of a hand, in or out of terrarium. In this position the forelegs, including tarsi, are extended straight forward, parallel with line of body, head and antennae tilted back. When touched, the insect breaks the stick formation, rearing the prothorax slightly with forelegs flexed. With continued teasing he tries to run. Although he can run fast intermittently, there is little or no jumping and he is apparently not as skillful a dodger as any of the mantids previously discussed. The stick position can be induced only two or three times in a single experimental session; after that, there is escape behavior. The following elements of mantis defensive behavior are absent: swaying, teetering, striking, jumping, tegmina and wing-lifting; abdominal lifting, twisting or twitching; antennal vibration. When the insect has been much teased, the wings are fluttered slightly.

In females, both adult and preadult, the stick formation is assumed much less readily and completely than in the adult male; often, although both forelegs are extended to the front, they are neither closely apposed nor completely in line with the body; tarsal flexion is various and the head and antennae are tilted backward scarcely if at all. In addition the stick position is never held for longer than a few seconds. When closely threatened, the mantis drops easily; jumping apparently absent.

5. CATAMUSONIA sp.

(Plate II, Figures 6, 7)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 249, Pl. III, Figs. 10, 11.

Rest Position and Locomotion.— Male: typical stick rest position, the forelegs apposed and partly extended. Alert and active, an excellent jumper and a strong and ready flier. Female: usually rests vertically, head down or up, on green or greenish leaves or stems. Slow in all motions.

Defensive Mechanisms.— General types: primary, immobility with stick formation; secondary, escape.

Male: when first confronted with a lizard (*Polychrus*), *Catamusonia* froze, going into a perfect stick position, the foretarsi more or less flexed and the head and antennae tilted back. It watched the lizard, turning its head with the reptile's passing. Finally it dodged and flew in one motion. All subsequent tests showed that it takes to wing rather than drops in escape, and flight is the usual response to teasing. In eluding hand capture, it jumps. When seized, it rakes with the forelegs and tries to bite, while the wings are sometimes partly raised and the long, projecting abdomen curled up and down, the whole being twisted to the right side. The effect is that of an attempted sting but also similar to the usual abdominal pulsations of mantinid mantids. There was never a trace of display with mere teasing or other stimuli, however, although the test was repeated on other days and with various sequences of stimuli.

Female: although alert in the presence of a threat, such as a lizard, the female's responses are much less complete stick responses, but immobility, except for the slowly turning head, is absolute. The antennae and head are usually not tilted back, and the forelegs, although held straight forward, are not necessarily apposed; tarsal flexion, as in the male, is varied. On one occasion the mantis did not move while the lizard walked right over her; on the next circuit of the lizard she raised one leg, which was directly in the lizard's path, and the reptile passed underneath. Dodging is poorly developed.

When in the pre-adult stage, only the following response was seen to persistent teasing, including pressure on the sternum: the prothorax was reared, the jaws extended forward, the forelegs elevated high overhead and partly extended and the abdomen curved up. The position was held for minutes after cessation of the teasing. In this stage the stick position was never induced, despite numerous tests.

6. THESPROTIA FILUM (Lichtenstein, 1796)

(Plate II, Figures 8, 9, 10, 11, 12)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 250, Pl. III, Figs. 12, 13; Pl. VIII, Fig. 29.

Rest Position and Locomotion.— Resting position, preferably on tree trunks, underneath branches or hanging from twigs, usually gripping with four legs, the first pair being flexed and the thorax reared up; abdomen may be bent dorsally. When undisturbed walks exceedingly well on four legs; uses six when hurrying; sometimes teeters and sways in approaching prey; also may sway after eating or in pauses during exploring. In spite of the minute size of the first tibiae, the mantis seizes suitable prey, such as Microlepidoptera, skillfully, in the general manner of mantids, holding it capably in the angle between femur and flexed tibiae as it eats. Both adults and young often assume the stick position, described below under defensive behavior, during simple exploration.

The first instar young are fragile and weak, being poor jumpers and slow walkers. They often rest in semi-stick position, that is, with forelegs held forward, more or less parallel, but with an upward bend at the trochanter; the tibiae and tarsi are usually flexed. Alternately the forelegs are partly flexed under the body, the coxae being held at right angles to it. In walking and during pauses the next stage is sometimes assumed, with the coxae, trochanters and femora in a completely straight line; the head and antennae are never tilted back, however. The abdomen is held parallel with the line of the thorax but the whole body slants slightly upward from abdomen to tip of forefemora; sometimes in ordinary rest the prothorax is bent up, the abdomen held parallel to twig or slightly bent, too. The very young insect walks steadily but slowly on all six legs, except rarely; later in the same, first instar, it walks usually on four; it often sways slightly in exploring, as do the adults.

Defensive Mechanisms.— This is as good an example of a "stick insect" as any phasmid "walking stick," both the dull brownish coloring and the exaggerated elongation of thorax, abdomen and forelegs blending magnificently with a twiggy environment. The only cause for surprise, when this insect is seen in its natural habitat, is to find it so often on tree trunks or hanging from rather large branches. Although it is inconspicuous in such a place, it is practically invisible among dried vines, weeds or bushes; it is often difficult to locate even in a small terrarium furnished with suitable perches.

This species goes easily and repeatedly into a perfect stick as the primary type of defense; the second type is escape; actual striking is a rare third.

In defensive behavior the stick position seems to be induced most often by a sudden movement of a nearby object at an optimum distance of about three to six inches. However, as has been said, the position is often assumed during simple exploration of strange terrain; in many of these tests no moving object was present, the observer having been completely hidden.

In defensive stick behavior the insect always appears undisturbed by a lizard or human movement at eight inches, frequently continuing to groom; however, occasionally no response is made to sudden close movement except simple immobility even when the disturbance is as close as three inches. The size and form of the disturbance appear to have little importance. Immature and adult *Thesprotia* have been seen to go into stick position at the sudden flight of two small moths near them, inside their terrarium, the moths having wingspreads of about 15 mm — barely too large for the mantids to eat. These *Thesprotia* and more than 20 other individuals reacted similarly to stimuli as varied as lizards, monkeys, human hands and pencils, all manipulated with the human observer concealed. Releasers will be discussed more precisely in the general discussion on p. 282.

In assuming the stick position, the mantis straightens its entire body longitudinally, the closely apposed forelegs are extended straight to the front except for flexed tibiae and tarsi, so that a perfectly straight line is formed with thorax and abdomen. In less perfect formations, the abdomen is bent dorsally. Usually the assumption of the stick position is signalled by the tilting of the head backward, while the flexing of foretibiae and tarsi is the last part of the pattern to occur. The body is held completely rigid, even the feet sometimes remaining immovable when a lizard passes right over them. Nevertheless the insect remains alert, turning the head to watch the distraction, swaying almost imperceptibly outward and away from the threat or sidling with extreme slowness around to the opposite side of a stick during the passing; it also may adopt the stick position during walking or climbing, moving very slowly and intermittently, with the forelegs still stretched forward and the head turned as necessary.

If the insect is approached suddenly within an inch or so, however, or touched, whether or not it has been in stick position, and especially when it is in a fairly enclosed space, it rears the prothorax, flexes the forelegs and elevates the abdomen. Swaying may occur at the beginning of eating or when danger is past, or sometimes, when disturbed slightly, during moving away. If the disturbance continues it may strike briefly, but usually tries to escape as fast as possible and not in stick position.

When the threat is a gradual one, such as a slowly approaching lizard, the usual first response is immobility, unaccompanied by the stick position. As the approach continues and passes the insect usually sidles almost imperceptibly around to the underside of a branch or out of the way, with or without slowly assuming the stick form; it then drops to the ground where it either remains motionless, in or out of the stick position, or runs rapidly away. Males are good, though not strong, fliers, always flying upward; however, except when actual attempts are made to catch them, they do not fly when disturbed but behave as do the females and do not use the wings even to break the fall in dropping.

There was never any trace of wing display in the male nor, in this sex, of outspread forelegs with rearing, swaying and elevated or twisted abdomen in the presence of threat.

Post-embryological Development of Defense Behavior.— When disturbed, the first instar young shows no special adaptation to defense. When presented with a small lizard of suitable size to use *Thesprotia* as prey, the insect takes no apparent notice either when it approaches the lizard to less than an inch, or, vice versa, when the lizard passes practically touching it. There is no immobility and no assumption of the stick position. When it is teased directly by a pencil or fine brush, it simply tries clumsily to turn and get away, whether on a twig or on the ground; it is a very poor dodger, does not climb on the attacker and does not strike. When directly prodded it may rear up somewhat, but apparently only as a result of the mechanical pressure upwards on the sternum, and it turns and wanders away as soon as possible. Altogether, it appears the weakest and most defenseless of any of the young mantids studied.

During the second instar immobility and perfect sticks, including tilted heads, can be induced in some individuals and not in others. Apparently the stick behavior is in the formative period and needs a particularly strong, particularly sudden stimulus to set it off. Also there is undoubtedly individual variation even in members of the same brood. Dodging is much better developed than in the first instar.

By the third instar the stick position is easily assumed and the escape response well developed; as in the adult, the young mantis dodges and drops well, walks quickly and when teased stands its ground much better than in the first and second instar. Also, it tends to climb directly on the threat instead of clumsily running away; no striking, however, ever occurs. As in the adult, there is never a stick response to direct touching; that occurs beforehand, in response to a sudden close movement of appropriate size.

In one individual of the third instar a unique example of kataplexy was observed, the only case in any mantis in this study except *Acanthops.* The mantis, measuring about 11 mm, was in a terrarium with a 27 mm lizard. The mantis had been transferred quietly, and apparently undisturbed, on a stick from her own terrarium, and after some preliminary exploring of the strange surroundings climbed back on it and remained there grooming. I stirred up the lizard, on the far side of the terrarium, and as he approached the mantis went through the complete adult defense routine: it went into a perfect stick, including back-titled head and antennae; the head, however, was as usual moved to keep the lizard's head in sight. When the lizard got within one inch and became aware of the mantis, he suddenly snapped at it. Whereupon the mantis broke the stick position, made a lightning turn obliquely backward, raced across the terrarium and climbed high up on the glass wall. Then it promptly jumped or fell to the base of it, landing right side up and absolutely flat, with the forelegs in perfect stick formation and the others laterally extended stiffly, at right angles to the body. It was practically invisible to me. When I poked it gently after some moments there was no response. I then turned it partly over, whereupon it at once became active and ran away.

When presented with the threat of the large *Polychrus* lizard (430 mm), the third instar gave moderate defense responses but not as completely as to the small ones; there was some immobility but the antennae and head were not tiltd back during stick formation, nor were dodging, dropping or climbing on the threat so complete as before the small lizard.

In the fourth instar perfect stick positions are assumed with perhaps even greater readiness, during both defense and ordinary exploring, than in adults. Even when directly teased, the mantis does not break the stick readily, and when forced to dodge away it promptly reassumes the position afterwards.

Striking was not induced before the adult.

7. ANGELA QUINQUEMACULATA (Olivier)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 250, Pl. IV, Fig. 16.

Rest Position and Locomotion.— Adult male (unique specimen observed): the usual rest position is typically mantis-like, being upside-down, with the forelegs partly flexed. The posterior end of the abdomen, which protrudes beyond the wings, is usually curved dorsally in a shallow bow. In resting and walking there may be a slight lateral sway. The specimen was first noticed as it alighted vertically on a brown twig with the head up. In experimental work it proved, surprisingly, to be a strong flier, in spite of its clumsily fragile appearance.

Defensive Mechanisms.— General types: primary (possibly secondary): immobility with stick formation; secondary (possibly primary): escape.

In twelve tests in a room before a large glass window, the response to disturbance, whether touched or not, was prompt flight obliquely upward toward the light. No bright color flash was seen. Half of the tests were made with the large lizard *(Polychrus)*, half with sudden motions of pencil or finger. After the immediate flight response was exhausted the mantis dodged capably and tended to climb on the threat. Finally, when the mantis was resting on the underside of a twig, I very suddenly jerked my finger tip past him, several inches from his head (apparently exactly as had been done several times before). At once the mantis assumed complete stick position, the forelegs extended in front, closely apposed, the tibiae and tarsi flexed, the head and antennae tilted back.

When again tested, however, the following day, in the even, natural illumination of the insect house, the order of responses was exactly similar to that of most mantids: when the insect was not touched by the disturbance, the first response was rigid, complete stick formation which was maintained, except for appropriate, slithering dodges to the stick's underside, whenever the lizard touched or passed over it. On one occasion it jumped obliquely over the lizard's body, a good four inches, and then dodged around to the underside of the twig. There seems to be no doubt but that the flight responses indoors before the window were the result of strong phototropism. Unfortunately the insect died a few days later before further checks were made.

There was never any trace of display or attack under any provocation except for the following incident. One night the cage cover was suddenly lifted and a new perch hurriedly put in place, whereupon the insect, which was resting upside down against one of the screened sides, raised tegmina and wings abruptly and held them open for a few seconds without fluttering away.

Corroborative evidence on stick formation in the genus was obtained independently by Hughes-Schrader (personal communication), who observed females of *Angela* sp. taking the stick position in the field. The specimens are recorded by Beebe, Crane & Hughes-Schrader, 1952, p. 250.

8. Acontiothespis multicolor (Saussure, 1870)

(Plate III, Figures 13, 14, 15, 16; Plate X, Figures 43, 44)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 250, Pl. I, Figs. 4, 5; Pl. VIII, Fig. 32, right; Text-fig. 1, C, D, E; Text-fig. 2, A, B.

Rest Position and Locomotion.— This species is the most active and "nervous" of the local mantids. As an adult it tends to quick and frequent movement which resembles that of many species of young. The antennae usually vibrate rapidly, not only during exploration or disturbance, when the motion is constant, but during much of the periods of rest; the insect sways frequently from side to side, regardless of whether it is about to jump or when stalking prey. The resting position is always with the prothorax reared up and the forelegs flexed; frequently the insect hangs thus to the underside of twigs.

During the first instar, the antennae are in apparently unending vibration, held vertically and arching outward while the abdomen is held horizontally (Plate X). At rest, the forelegs are held closely flexed, the coxae hanging perfectly vertical.

In the fifth instar appears a special motion which is maintained, though less frequently, in the sixth, but is absent in the adult. It is apparently exploratory in character and consists in moving the forelegs alternately and almost constantly when in a strange place; the motion is of a revolving nature, somewhat like the motion of a boxer's "wind-up." (cf. *Promiopteryx*, p. 248).

Defensive Mechanisms.— General types: primary, immobility; secondary, active escape; tertiary, display.

The morphological specializations for the primary defense, immobility, are almost altogether concerned with the disruptive coloration pattern of green and buff. As usual, the immobility response occurs only when the mantis is not actually touched, but becomes aware of a disturbance a few inches away. There is no special flattening preceding the immobility. When approached closely or touched by a lizard, pencil, finger, etc., from the front, its usual response is to run toward and climb on the threat; I have not yet seen a specimen take to flight. Jumping is rare. The antennae during threat are in a constant state of the most rapid vibration, whether or not the insect is otherwise motionless, the vibrations being so rapid that the organs are practically invisible.

Display has been seen only three times, and in the same individual, a female. It occurred first when I suddenly thrust my hand into the terrarium and started to pick the mantis up; immediately thereafter she displayed again, outside the terrarium on a stick, when presented to the test lizard. Afterwards, when returned to the terrarium, it continued for a time, even though undisturbed. Another day, she displayed when confronted by the lizard in the insect house. The mantis then sidled around the stick, dropped to the ground and ran off. But a third day, neither it nor another female displayed to the lizard, each remaining motionless at a distance of about three inches for more than a minute. At the end of that time the lizard in both cases moved forward, rather slowly, and ate the mantis. (Plate III).

In display, the prothorax is raised, with forelegs extended laterally, while the tegmina and scarlet and black wings are elevated. The abdomen is raised scarcely or not at all and is not twisted; it is noteworthy that it lacks distinctive coloration except sometimes a rosy wash basally. The insect sways violently from side to side, turning the head and thorax so that the scarlet of the wings is visible from the front. The antennae continue to vibrate rapidly. The jaws are not opened and there is no actual striking of the disturbing object.

Post-embryological Development of Defensive Behavior.— Throughout the early nymphal stages the emphasis is on active escape rather than on freezing. Leaping to twice the length of the nymph is frequent. In the first instar, where the coloration is pale brown, chestnut and dark chestnut, the general appearance is very antlike; the habit of running rapidly on all six legs enhances the effect, although they frequently jump when disturbed. By the fifth instar little apparent attention is paid to an approaching disturbance until it is touched by the tip of the mantid's antennae, when the insect rears and reaches out with its forelegs, alternately in rapid succession. When a surface is thus grasped the insect climbs upon it. Unfortunately observations concerning the instar at which freezing first occurs have not been made, except that it is not developed in the first and second, and, if it occurs at all, is certainly rare before the pre-adult. Striking was never seen in the young, any more than in the adult.

9. Tithrone roseipennis (Saussure, 1870)
(Plate IV, Figures 17, 18, 19; Plate X, Figure 45)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 253, Pl. I, Fig. 3; Pl. VIII, Fig. 32, middle; Text-fig. 1, F, G, H; Text-fig. 2, C.

Rest and Locomotion.— Resting position with the prothorax slightly reared, abdomen horizontal, forelegs flexed, usually on vertical stem or on underside of twig. Walks moderately rapidly, jumps occasionally in ordinary locomotion to cross gaps only; does not tend to fly when undisturbed. At rest antennae are quiet; in a strange environment they vibrate moderately to rapidly.

In the first instar the general appearance and normal behavior is that of a small black ant; all six legs are used in walking much more than in the adult; the forelegs are completely flexed infrequently during rest; it runs rapidly but in short spurts, often rearing high in the pauses. Sometimes it sways far from side to side, sometimes rearing prothorax simultaneously. It can cling tenaciously; it is an excellent jumper, and can leap a distance of at least eight times its length on a horizontal surface, although it jumps but rarely. The entire abdomen is almost always bent sharply up; only occasionally, during exploration, is it held for a short time horizontally. The antennae are so slender and in such constant vibration that they are almost invisible, a characteristic which, combined with the abdominal position, heightens the resemblance to an ant.

In exploring, the forelegs, at least through the second instar, are partly extended and retracted, alternately or in unison; however, unlike *Promiopteryx,* they are always divergent; even when held flexed at rest the coxae diverge. (Cf. also *Acontiothespis*).

Defensive Mechanisms.— General types: primary, immobility; secondary, escape; tertiary, display.

The usual response in the face of a strange object of medium size moving at a distance of three to six inches is immobility. This is preceded by a slight flattening; during the period of freezing the antennae vibrate so rapidly as to be practically invisible. The scarlet wings are completely hidden and the leaf-green insect enjoys in its usual habitat adequate though unnoteworthy concealing coloration. If the threat, such as a lizard, *slowly* approaches more closely, the insect usually remains motionless as it is until the lizard actually touches it; then it may either sidle almost imperceptibly around the stem or branch, allowing the lizard actually to trample over part of it, or it may approach the threat and climb on top of it. Often the insect stops right there and grooms, or it may continue on down the full length of the reptile. Whether it avoids the threat or runs over it, it soon after drops or flutters to the ground. Frequently the slow-moving lizard has eaten the insect. On these occasions the mantis, judging by the crouched, immovable position and the swiftly vibrating antennae directed forward, was completely alert to the threat yet made absolutely no effort toward either escape or display.

Flight is apparently reserved for a swift-moving threat, when the insect is cornered at the tip of a branch or stem; it is never upward, but practically always obliquely down; when it alights it usually sits quite motionless for a few moments and then moves unobtrusively off. At the moment of spreading the red wings there is to human eyes a strong impression of flash coloration which is most effective in concealing the alighting position.

Display is much more difficult to induce in this mantis than in any others in which it is known to occur. Of the several dozen *Tithrone* tested, most individuals have never been made to display under any provocation. Several, however, have displayed one to three times, on different days, always only under strong stimulation consisting of a sudden rapid motion (by lizard, pencil or grasping fingers) toward them when in a somewhat restricted space such as a terrarium. One female alone displayed readily under these conditions for the entire two months in which she was kept alive, during which she laid four oöthecae. She was tested on a total of about ten days. No display lasted more than a few seconds, but once an insect displayed, up to four more displays might be induced quite easily within the following half hour.

Rarely, some of the non-displaying *Tithrone,* when hard pressed by the threat and before dodging or fluttering away, sometimes showed a bit of scarlet as the tegmina barely started to lift.

The full display consists of extending the forelegs laterally, raising prothorax, tegmina and wings, swaying from side to side, and twisting posterior thoracic segments and abdomen to the side, the abdomen's lateral edge tilted uppermost, so that the scarlet wing-surfaces and dorsum are presented to the threat. The antennae vibrate and the black mandibles are sometimes widely extended. In less than full display, the abdomen is jerked up and down, not twisted laterally, while the forelegs remain flexed and the mandibles closed.

Post-embryological Development of Defensive Behavior.— At least throughout the first and second instars, escape is the only response to threat and even this activity is poorly organized, with no apparent awareness of the threat until it is actually touched. Then it usually turns around and retreats, instead of mounting the threat or dodging as do older stages. There is absolutely no trace of freezing in either first or second instars. Its exact time of appearance has not yet been determined. During these earliest instars there was an apparently complete lack of awareness even of an actual enemy, such as a moving 27 mm *Gonotodes* which ate a number of the young from time to time. The young mantids would move about in any direction, make exploring motions and groom until the moment the lizard snapped.

10. ACANTHOPS FALCATA Stol, 1877

(Plate IV, Figure 20; Plate V; Plate VI; Plate X, Figure 46; Text-figure 1)

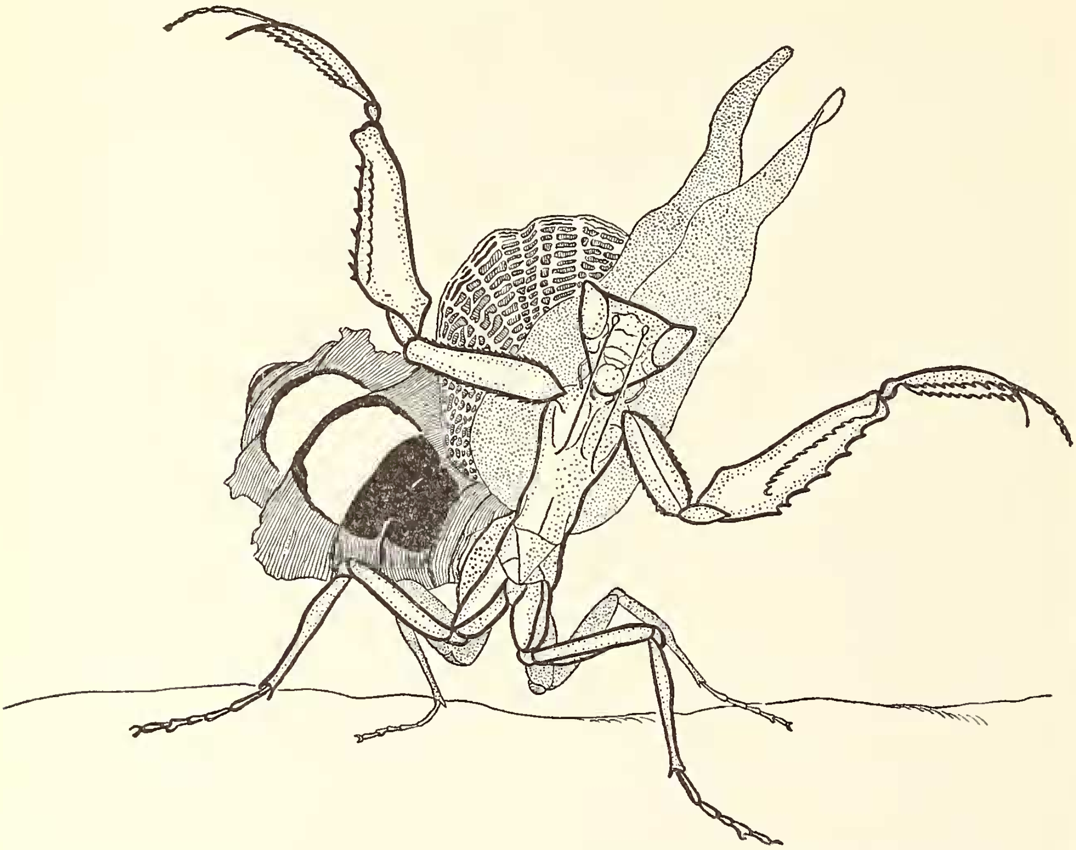
Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 254, Pl. IV, Figs. 14, 15; Pl. VIII, Fig. 31.

Rest and Locomotion.—Male rears up seldom when in rest position, usually clinging vertically to upright twigs and stems; female's normal rest position is hanging from underside of more horizontal twigs, the prothorax strongly reared, abdomen bent dorsally, forelegs completely flexed. They move deliberately, more so than the males, trembling and teetering with every step and usually walking on the two posterior pairs of legs. Both sexes are poor jumpers; the females do not apparently fly or flutter when undisturbed; the males fly capably but seldom.

In the first instar the dark brown, small mantids are already unmistakably *Acanthops* in general position and appearance. The resting position is as in the adult, V-shaped, with the head and thorax forming one arm and the sharply upturned abdomen the second, shorter arm. However, they have none of the adult's apparent "poise"—their slowness to move and to be startled, their almost instant "tameness" in a strange environment. On the contrary, they are very active and vigorous and are good leapers. Teetering and swaying is common from hatching, both at rest and in exploring.

Defensive Mechanisms.—General types: primary, immobility, associated with a strong protective resemblance to dead and shrivelled leaves; secondary, active escape; tertiary, display; quarternary, striking, or kataplexy.

In this mantis the resemblance to a dead leaf, or rather to a pair of dried and shrivelled leaves, is carried to a fantastic extreme. This is particularly true in the female. It has been recently cited as an example by Chopard, who says (1938, p. 126-127): "Toutes ces mantes" (resembling dried leaves) "sont de coloration brune plus ou moins rougeâtre, leur prothorax est élargi, leur élytres a l'aspect foliace, leurs pattes plus ou moins lobées. Chez les *Acanthops,* qui sont sans doute les plus curieuses, le bord des élytres est échancré comme le bord déchiquet d'une feuille, le corps est couvert d'asperités, et l'abdomen est élargi, ses bords dilatés en forme de lamelles. L'ensemble est tout à fait remarquable et semble bien propice à assurer la dissimulation de ces Mantes au milieu des feuilles mortes. Une seule ombre au tableau: on ne sait pas du tout dans quel milieu se trouvent les *Acanthops;* on peut tout de même supposer que ce sont des Mantes de forêt; mais peut-être vivent-elles parmi les



TEXT-FIG. 1. *Acanthops falcata* ♀ in full display. Wings yellow and black; abdomen rosy red and black; color otherwise brown. Minor spinulation and modeling of tegmina simplified. Body length in life, *ca.* 41 mm.

feuillages verts où leur homotypie serait bien moins remarquable."

Chopard's concern over whether or not *Acanthops* occurs only among dead leaves, though valid in the temperate zone, is not generally applicable in the American tropics, in the habitat of *Acanthops.* For here the rainfall distribution and amount supports rainforest, or, at least, semi-evergreen seasonal forest; where these climax formations have been replaced with second growth or scrub—a typical *Acanthops* niche—the vast majority of plants normally bear both drying and shrivelled leaves along with the green throughout the year, not to mention the usual high tropical quota of partly eaten or otherwise damaged leaves. Therefore a motionless brown insect dangling from a twig, especially of the leaf-like form of *Acanthops,* would not usually be in the least conspicuous even though resting among a majority of green leaves. In both Venezuela and Trinidad I have observed probably half a dozen undisturbed individuals of this species in the field. In each case the mantis has been on twigs or stems among fairly small leaves, including dicotyledonous weeds, bushes or low trees. In every case dead and damaged leaves were present but did not predominate. Also taken by Hughes-Schrader in tangles of dead branches and vines (Beebe, Crane & Hughes-Schrader, p. 254).

In the female *Acanthops* the tendency to sway is carried to extremes, particularly when the twig is lightly shaken; it takes the form of a more or less violent trembling and resembles perfectly the motion of a dried leaf in the breeze. However, it occurs equally when there is no wind, and when the insect is either walking or stalking prey. The uneven motion, however, is very possibly helpful in making the insect inconspicuous. Upon analysis, the swaying and teetering motion consists of three separate parts: first, lateral swaying of the prothorax; second, vibration of the abdomen in the vertical plane; third, lateral teetering of the body on the second and third pairs of legs. The most essential element, the first to appear and the last to cease, is the abdominal vibration.

When first disturbed, but not touched or threatened by a sudden movement, both sexes invariably become immobile. In the adult, however, there is never any approach to a stick position, in contrast to its occasional occurrence in the young, which is described below. If the threat approaches the male usually flies promptly and capably upward toward the light, at a steep angle; on alighting he becomes motionless at once. The female on the other hand may either walk slowly away, generally away from the disturbance, or, more usually, sidles around to the lower side of the perch if she is not there already, and drops promptly to the ground. More rarely she approaches the threat and climbs on it, as with other mantids.

Display, the tertiary line of defense, is almost entirely confined to females. Here it is one of the most striking and easily induced in any of the local mantids. All of the usual elements of full mantis display, except opening of the mandibles, are there: both prothorax and abdomen are elevated; the forelegs are widely extended laterally; tegmina and wings are raised; the shiny, brightly-banded abdomen is twisted to the side and tilted, filling in the space beneath the wings, which are unevenly elevated so that both may be seen; finally, the entire insect sidles and sways violently from side to side. A characteristc display motion is the downthrusting of the antennae, which do not vibrate or wave. It serves, in fact, as a motion of intention, since it precedes elevation of the wings. Several times, after a prompt display to a lizard, females have swung to the lower side of a branch and dropped to the ground just as the lizard passed overhead. A lizard or snake has never yet been seen to snap at a displaying mantis.

Male *Acanthops* have been induced to display only twice. In each case the stimulus was a sudden motion toward them when they were in the enclosed space of their terrarium. The performance was exactly like that of the female, but the effect was ludicrous in comparison, since the wings and dorsum are plain dark brown instead of with the yellow, black and rose-red accents of the female which are to human eyes so striking. Each male display was brief.

Very rarely, when very hard-pressed, both sexes will strike out with the forelegs, whether or not they are displaying. The alternate behavior for this quarternary line of defense is kataplexy. This occurs only when the insect is suddenly touched or grasped, and is complete: the insect suddenly becomes completely motionless and inert, with the legs all drawn in close to the body; it remains in this condition for from a half to several minutes and can be kept there indefinitely simply by touching it at intervals. I have never been able to induce this condition in the three males tested, but most (not all) females assume it readily.

Post-embryological Development of Defense Mechanisms.—The development of the remarkably varied defense mechanisms in *Acanthops* is of special interest. Not only does the time of appearance of the factors vary in different individuals, but one factor—the stick position—occurs only in the young. Enough data has not yet been assembled to determine whether or not there is a sexual dimorphism in the development of the traits.

As in most mantids, in the first instar there is usually little apparent awareness of threat. In the very rare instances where the mantis definitely turns its head to keep a nearby lizard in view, exaggerated teetering and swaying are the rule; this distinctive movement would doubtless be conspicuous even if the mantis were in its natural environment. The usual response to a particularly close, sudden, swift-moving threat—usually at a distance of less than half an inch—is a simple and undirected running away, without dodging or climbing onto the threat; this also is accompanied by rapid teetering and swaying and sometimes by jumping or dropping.

In rare first instar individuals, however, one of the following types of behavior in the face of threat has been recorded. First, freezing. Second, freezing accompanied by a well-formed stick position, in which the forelegs are stiffly extended and apposed, the tibiae and tarsi being flexed back along the femur; unlike true stick mantids, however, neither head nor antennae are bent back. Third, depression of the antennae when closely approached by the smallest test lizard, a 27 mm *Gonotodes.* Fourth, brief but perfect kataplexy was induced in one individual after its escape from the lizard when I made a sudden motion with the forceps; the same response occurred several times. Only a single one of these rare first instar responses was induced in any individual, but three of them were found in individuals of the same brood; all of them were subjected to test conditions made as nearly identical as possible. Altogether about thirty individuals of five broods from three females have been tested.

The subsequent development of these and the remaining display characteristics is also rather irregular. The downthrusting of the antennae, before the adult display stage, was induced throughout the subsequent instars, but only in response to small lizards or snakes, never to other threats such as forceps, pencils or fingers. The odor of a reptile (such as may confront a mantis in a lizard's empty terrarium, on his just-vacated perch) had no effect on the antennae. Similarly, no effect on the antennae was produced by the largest lizard, a *Polychrus* more than a foot long, at any stage before the pre-adult. In the adult, regardless of the stimulus situation, downthrust antennae are the regular concomitant of display, as already described.

Freezing occurred irregularly but with increasing frequency until the fifth instar, when it became the rule as in the adult. The assumption of a stick position is rare throughout development, was induced only once in the pre-adult, and never in the adult. Kataplexy is rare and sporadic throughout until the adult female. When it does occur, however, it seems to be easily induced in that individual indefinitely. In one insect, a female reared from the egg, it was first observed in the fifth instar, and after that occurred almost daily when the insect's jar was cleaned; this individual died in molting to the adult. In other specimens, including several sisters and brothers which completed development successfully, kataplexy did not appear until the pre-adult, or never occurred at all. Striking, rare even in adults, was induced once in a pre-adult female which was being teased with a black-handled camel's hair brush.

The first trace of a display-like tilt of the abdomen occurred in several pre-pre-adult specimens (fifth instar); it occurred during a freeze position in front of a small lizard, and was accompanied by downthrust antennae and a very slight vertical vibration of the abdomen. The latter, though bent to the right of the vertical, was not twisted as in the adult, nor were the forelegs spread laterally.

11. PARASTAGMATOPTERA VITREPENNIS Bruner, 1906

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 254, Pl. V, Figs. 18, 19.

Remarks.—Only a single male was taken. Because of its great rarity no tests or observations were made outside its terrarium. It rested in typical mantis position, forelegs folded, usually on underside of twig; the prothorax slightly reared. It was not active, fluttered or climbed to the bottom when disturbed, did not strike, go into a stick position or show any signs of display when teased with a pencil or finger, pinched, or otherwise disturbed. No lizard or other living threat was used. Although it appeared uninjured and ate well, it died on the third day.

12. STAGMOMANTIS CAROLINA (Johannson, 1763)

(Plate VII, Figure 29)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 255, Pl. VII, Figs. 24, 25; Pl. VIII, Fig. 33.

Rest Position and Locomotion.—Usually rests on underside of twigs or branches, prothorax reared, forelegs flexed, abdomen flat. Walks on either four or six legs; jumps rarely and heavily.

First instar young: rest position similar to that of adult, but abdomen, in both rest and locomotion, more or less erected. Antennae active but not to the point of vibration. The young are exceedingly active, being very rapid walkers and climbers as well as strong and skillful jumpers; they do not, however, exhibit the extreme activity found in *Tithrone.* In exploring they rear high up and peer around, often swaying, especially before jumping; they are strongly phototropic and negatively geotropic.

Defensive Mechanisms.—General types: primary, immobility; secondary, escape; tertiary, display; quarternary, attack.

Both the green and the brown phases, though so different, enjoy excellent general concealing coloration. The first response to general, non-sudden disturbance of moderate size, such as alertness to a lizard a foot away, is complete immobility in whatever position the mantis happens to be—legs at odd angles, forelegs partly flexed or not, head turned toward the disturbance and following it. The antennae are laid back, parallel. The next phase is the usual inconspicuous sidling around a branch and dropping to the ground, the fall broken in the case of females by fluttering wings, or the male may take to true flight, generally with a preliminary downward drop. The brown-phase males, the only ones taken, in about half the tests omitted the preliminary immobility and took to flight at once. At first, when the insects were freshest, flight was more frequent than freezing. In flight the rosy dorsum of the male was not conspicuous, nor, of course, were the hyaline wings; therefore there was no flash effect. In both female color phases, however, the wings—red or yellow—were striking in the flutter to the ground.

Readiness to display varied considerably among the four adult individuals captured or reared to that stage. All were induced to display at least twice under the usual conditions—sudden teasing, grasping or motion downward, especially in a confined space, or after preliminary eliciting of immobility-escape sequences; the display was once drawn, for instance, when the mantis was teased with a pencil on the ground after she had dropped down from a lizard's vicinity.

The dark phase female was for several weeks exceedingly prone to display; after that, although she was kept for another month, she displayed rarely in spite of every provocation.

Display in this species has all the elements of fully-developed mantis display except that the abdomen is not twisted laterally; hence the dorsal surface cannot be seen from the front. Instead the tip is curled up between the wings and is quite invisible; however, the second and third thoracic segments and the abdomen generally are turned slightly sideways from time to time, presenting the red and yellow wing surfaces to the front. For the rest, the antennae are usually laid back, parallel, but are sometimes erect and divergent; the prothorax is erected; the forelegs, in full display, are twisted and extended laterally, bent up at the trochanter, the tarsi flexed; this position shows the black sternal bar most effectively. The tegmina are elevated, the inner margins brought close together posteriorly and the outer separated and farther forward; this position makes the tegminal spots inconspicuous because of the angle of view from the front; as usual, the left tegmen is higher than the other, filling in the space completely between prothorax and the erected wings. Sometimes there is considerable swaying from side to side; at others the insect stretches on tiptoe and sinks alternately; still again the pose may be held motionless. Sometimes only the tip of the abdomen quivers up and down. Once, one of the green females did not display completely, but raised only the wings, the tegmina remaining flat, and, just before she started to lower them, vibrated the wings with an audible rustle; this vibration was not observed again.

Rarely after display, in the face of continued threat or teasing, the insect pulls in the forelegs and strikes strongly and repeatedly. It will also both grasp and bite if suddenly picked up and held.

Post-embryological Development of Defensive Behavior.—Some first instar young of *Stagmomantis* have more elements of adult defense behavior developed than any other species studied. However, there is a great deal of individual variation, even among members of the same brood. At its optimum expression, the just-emerged mantids are alert to a 2-inch lizard, moving up to 8 inches away, and follow through the freeze-and-watch, dodge-and-drop, sequence of the adult with great facility. During full freeze the antennae are bent back and laid closely together; the head alone moves slowly, keeping the lizard in view. One individual froze promptly at the sudden close flutter of a small moth with a wingspread of half an inch. None ever appeared aware of a foot-long *Polychus* under any conditions, and hardly ever of a 4-inch lizard. Instead of dropping from a threat, these very young examples sometimes, after freezing and dodging, make high jumps almost vertically upward, such as one measured from the floor of the terrarium a full eight inches up to the rim. Similar jumps have been noticed up tree-trunks when they were startled in the course of being released in the field. Several young actually struck at a fine-pointed white probe, several times in quick succession, in the fashion of adults, before dodging to escape. Retreat does not occur in the most advanced of these first instar individuals. Apparently even the most precocious do not climb on the threat, do not extend the forelegs or sidle in the fashion of display; these traits are not developed until the middle instars or later.

Other individuals show defense patterns of a rough simplicity equivalent to those of the young of other genera: there is little or no evident awareness of a threat, immobility and dodging are absent and when actively attacked the mantid simply turns clumsily and tries to run away; there is no trace of striking. In one individual, reared successfully to a healthy adult male, the pattern was not even well developed by the second instar (17 mm). On one test day, the following notes were made: "When presented with the 12-inch *Polychrus,* the mantis went on grooming at eight inches, but suddenly became immobile; when the lizard approached slowly to 1.25 inches there was still no motion. But as the reptile passed, the little mantis slid around to the lower side of the branch and continued to hang motionless. When the lizard was gone from sight, the mantis swayed slightly, the abdomen was raised, and the insect groomed. After several minutes more, it walked off. The antennae had remained erect and divergent, not bent back, throughout."

Two days later, in the same instar, "on six trials the insect apparently completely failed to respond to the lizard as a danger; it groomed, ran toward him, teetered, climbed on, over and around it repeatedly. There was no freezing, no dropping, no jumping, no 'purposeful' running toward and onto the lizard. The mantis could have been eaten at leisure over and over. On the seventh test, as the lizard passed just ahead of him, a front foot beside him, the mantis did apparently become aware of the threat and seemed to freeze. This time, however, there was no flattening, the insect remaining reared up as he happened to be at the moment, the forelegs and other legs sprawled every which way, the abdomen curved in the usual rest position; the immobility was held only fifteen seconds, after which the insect groomed; then it climbed on the lizard's leg, perched on the eye, and resumed grooming."

These two rather detailed descriptions of opposite behavior in the same instar toward the same threat under conditions as closely similar as possible, indicate both the variability of mantis behavior and, most interesting, the apparently as yet unfixed form of the freezing-dodging mechanisms. They are examples of many other cases of similarly "erratic" behavior which is particularly noticeable in young mantids of all species studied, and occurs before threats, regardless of size.

During the final instars before the adult (sixth and seventh), these mantids are still excellent jumpers, especially when disturbed. They resemble the adult in their increased tendency to lunge, strike repeatedly and even bite when closely threatened or teased; they have by now also developed the trick of rapidly approaching and climbing onto the threat.

When presented with a monkey, a pre-adult female turned around and fled repeatedly. The same individual, however, a few minutes later when confronted with a katydid bulkier than itself, reared, elevated the abdomen sharply and vibrated it, flexed the forelegs, and, when the katydid was two inches away, struck out strongly. Before and after each strike the forelegs were held with the inner surface twisted forward. In walking after a strike the mantis invariably swayed slightly. Each time during nine tests the katydid gave ground. The mantis never made any attempt to seize the other insect or to bite.

13. STAGMATOPTERA SEPTENTRIONALIS Saussure & Zehntner, 1900

(Plate VII, Figures 30-34; Text-figure 2)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 255, Pl. VI, Figs. 22, 23.

Rest and Locomotion.—Resting position with prothorax reared, forelegs flexed, generally hanging from underside of branch. Teeters frequently in walking, on four legs or six. The male is a very strong flier, soaring up and out over the tree-tops and out of sight when released or allowed to leave terrarium; this was observed five times.

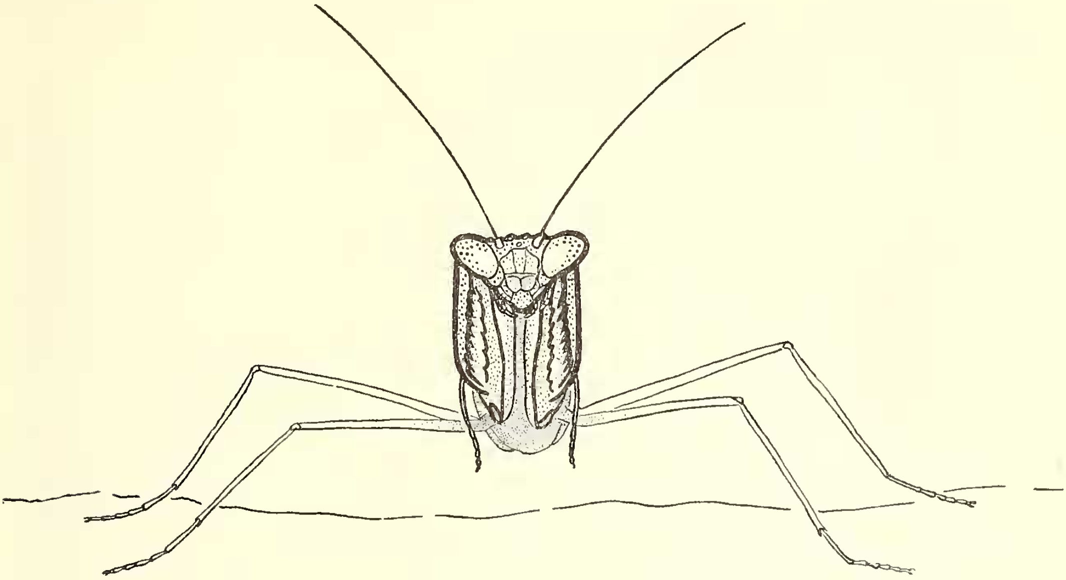
Defensive Mechanisms.—General types: primary, immobility; secondary, escape; tertiary, display and/or active attack.

The usual sequence in an adult male is, first, immobility, then sidling away from the line of approach of the threat, for example to lower side of branch, then usually a further period of immobility, and finally a fluttering down to the ground.

Display is likely temporarily to replace escape under the following conditions: first, when the mantid is threatened in a confined space; second, when the threat is actively stalking the mantid at close range; third, when the stimulus of a quiet threat, such as lizard or monkey, is reinforced by the teasing of forceps or fingers; fourth, when the mantid, after one fluttering escape, is promptly confronted with the same or a different threat.

Attack frequently supplements or replaces display at very close range. Test lizards and monkeys have been both struck repeatedly by *Stagmatoptera.* Twice a lizard has been seen to turn tail and go away; once one was almost knocked from a branch by the blow. A young monkey was also twice startled into full-scale retreat. After other attacks, the mantid followed up its opponent's hesitation by quickly fluttering away. The insect will strike also at a pencil, finger, large insect or any other moderate-sized threatening object too big to treat as prey.

Display: in the male, identical with that of *Oxyopsis* female described on page 277, except that at the peak of display neither the head nor the widespread forelegs are thrust backward, although the femora are rotated, showing the black spots; side to side swaying is a usual concomitant of display and the jaws are not opened. As in the display of *Oxyopsis,* the forelegs may be held in an alternative position, flexed in striking position; here especially the inner surface of the femora, with their conspicuous black spots, face forward, toward the threat. Held closely in this fashion, the two spots appear as one. The shiny wings and twisted, glistening, pulsating, yellow abdomen—all visible from the front as the insect sidles and sways—are a conspicuous sight from the human point of view; the tegminary stigma are also in evidence, since the tegmina are held straight up, their surfaces facing almost directly to the front. However, in this sex the spots are not nearly as strongly developed as in females, which we know personally only from Venezuelan examples taken at Rancho Grande. (At that time we were not working with mantids, but a motion picture made of a displaying specimen shows no distinguishable differences from the display of Trinidad males. The female's photograph in the present paper (Pl. VII, Fig. 30) was made at Rancho Grande, Venezuela). One male, in a partial display, made a distinct whirring sound with the wings, as occurred once in *Stagmomantis* (p. 275).



Text-fig. 2. *Stagmatoptera septentrionalis* ♂. Resting position from the front. Cf. contrasting conspicuousness of display position (Plate VII). Body length in life, *ca.* 73 mm.

14. Oxyopsis rubicunda (Stol, 1813) (Plate VIII, Figures 35-38)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 256, Pl. V, Figs. 20, 21; Pl. VIII, Fig. 32, left.

Rest and Locomotion.—Resting position and walking habits of female exceedingly similar to those of *Stagmatoptera* except that the short wings and heavy body make her a feeble flier, flight being apparently reduced to a groundward fluttering. The male flies capably but unfortunately no special observations were made on the single specimen taken.

Defense Mechanisms.—Except for attempts to induce display no observations were made in the male. No display resulted except once when the insect had been teased with a pencil. Then the abdomen was slightly raised, pushing the gauzy wings partway up.

The usual defensive behavior of the female, when confronted by a normal enemy (e.g., lizard or monkey), is to become immobile, then quietly slip around to the underside of a branch and either once more become immobile or flutter to the ground and run off. Display was induced on two occasions, once when cornered between the wall and a branch, faced with the lizard and simultaneously prodded slightly with a pencil; again, with the second female, by a sharp rap on her perch, close to her, and in plain sight. The circumstances in each case were duplicated as far as possible on other days and with both specimens, but without success. Once one female struck at the lizard, which turned around slowly and moved off. The two females were kept for a time together, after the molting of the younger to the adult stage. The older, larger one was dominant from the start, making attack motions at the young female which kept retreating into far corners of the terrarium. Several times the old one lifted her wings toward display position, the forelegs always being held closely flexed in attack position. The two mantids came to terms of some kind, with no damage done, after two days and got along for a week, until the younger one was preserved.

The display itself is as follows: head and prothorax elevated; antennae directed obliquely backwards, divergent; head turned in direction of threat, mouthparts widely open; forelegs extended laterally, widely separated, straight; at culmination of display they are even pushed backwards, almost to right angles of each other, and the prothorax similarly directed backwards, nearly touching tegmina. The latter are erected almost vertically, somewhat separated, the wings elevated and filling the gap between elytra and abdomen. The tip of the abdomen is curled up and down and the whole slanted to the left, so that its upper surface is obviously visible from the front. The display is, in color, exceptionally effective to human eyes, in spite of the absence of brilliantly and contrastingly colored wings:

the orange tips of the widepread forelegs and the brilliant orange and red palps with black (usually concealed) between, are exceedingly conspicuous. In addition, the pulsating yellow abdomen, twisted sideways, flashes in the light.

Several details of the display require comment. First, the small, double-centered tegminary stigma are quite hidden by the head during display and in any case are exceedingly inconspicuous.

Second, the sequence of display motions is especially evident in this species, from mere incipient display to its full expression. The first phase is a mere rearing up of head and prothorax with the tip of the abdomen slightly elevated but the wings closed; the forelegs may or many not be extended at this point and the mouthparts may or many not be expanded (i.e., forelegs may be open and jaws shut, or vice versa, or neither). In the second and final phase the tegmina are vertical, hindwings widely open, abdomen twisted laterally and twitched up and down, while the mouthparts are extended and the forelegs widespread, laterally and somewhat posteriorly. Not seen to strike.

Post-embryological Development of Defense Mechanisms.—Pre-adult female: in walking, using all six legs, teeters antero-posteriorly between steps. Rests usually upside-down, prothorax reared, abdomen bent or not. When cornered, flexes forelegs, rears prothorax moderately, elevates abdomen high and sways from side to side.

15. VATES LOBATA Fabricius, 1798

(Plate IX, Figures 39, 40)

Reference.—Beebe, Crane & Hughes-Schrader, 1952, p. 257, Pl. VII, Figs. 26, 27.

Mechanisms of Defense.—Since the single specimen, a female, was observed only for a day, the following notes are fragmentary. This species seems midway, in both appearance and behavior, between the green, aggressive *Stagmatoptera* and the quiet, inconspicuous, *Stagmomantis* male. In general appearance it tones in perfectly with the shadows made by dried and curling leaf-tips. The forelegs are often partially extended, parallel and closely apposed during immobility, that is, assuming an incomplete version of *Thesprotia's* stick position. The general types of defense appeared to be primarily immobility and secondarily active escape by means of the usual sidling and dropping technique. The individual was not seen to fly and did not display under any stimulus, including confrontation by a lizard.

IV. COMPARATIVE RECAPITULATION OF DEFENSE MECHANISMS

A. Adults

It will be seen from Table 1 that immobile reliance on background resemblance is the primary line of defense in all except two or three species, while active escape is the secondary. Startle display occurs in almost half the species and possibly but not probably in one or two more; the rare *Mantoida, Musonia* ♂, *Angela, Parastagmatoptera* and *Vates* were not tested adequately; their dull coloration, however, makes display very unlikely. Only four species were ever induced to strike or bite.

Table 2 shows that eight out of fifteen species depend on generalized, inconspicuous toning-in with the background in at least one sex, whether primarily green or brown, combined with simple immobility. This group lacks a specialized resemblance in structure, coloration and behavior to a particular part of that background. Two forms, the self-flattening *Liturgousa* and brown-phase female *Stagmomantis,* are hidden with particular success when resting against lichens on bark; the *Stagmomantis,* however, is counted in the category of general inconspicuousness since it does not usually occur on the specialized background.

Musonia females strikingly resemble small twigs, along which they range themselves vertically, sometimes at an angle, in complete or semi-stick-like positions. *Catamusonia,* although bright green in the adult, forms an equally satisfactory twig. In the exceedingly elongate *Thesprotia* and *Angela* the stick resemblance is carried to extremes; in these, even the head and antennae are flattened back into line with the extended forelegs and rigidly straight prothorax. It should be re-emphasized, however, that one of the most usual locations of *Thesprotia* is on tree trunks; it has been found even in such twigless locations as the broad green leaves of *Agave.*

Two perfect leaf-mimics are included in the group. These are *Acanthops,* which in both sexes but particularly in the female are fantastically like dried and shrivelled leaves in appearance, and *Oxyopsis,* which in the female bears an excellent similarity to fresh green leaves. Associated with *Acanthops* is a special movement or series of motions which in the optimum environment is an improvement on simple immobility during the primary dependence on inconspicuousness. This is the occasional vibration of *Acanthops* as it hangs from a twig, which closely resembles the trembling of a dried leaf in a breeze; unfortunately for the perfection of the adaptation,

TABLE 1. DEFENSE MECHANISMS OF ADULT TRINIDAD MANTIDS
(Numbers indicate relative importance)

	Protective Resemblance	Active Escape	Startle Display	Active Attack
Mantoida sp.*	2	1	–	–
Liturgousa sp.	1	2	–	–
Promiopteryx granadensis	2	1	–	–
*Musonia surinama**	1	2	–	–
Catamusonia sp.	1	2	–	–
Thesprotia filum	1	2	–	3
*Angela quinquemaculata**	1 (?2)	2 (?1)	–	–
Acontiothespis multicolor	1	2	3	–
Tithrone roseipennis	1	2	3	–
Acanthops falcata	1	2	3	4
*Parastagmatoptera vitrepennis**	1?	2?	–	–
Stagmomantis carolina	1	2	3	4
Stagmatoptera septentrionalis	1	2	3 or 4	4 or 3
*Oxyopsis rubicunda**	1 (female)	2 (female)	3 (female)	–
*Vates lobata**	1 (female)	2 (female)	–	–

* Observations incomplete.

Acanthops tends to tremble equally when there is no wind. Even so, any one familiar with tropical forests knows the frequently unaccountable swaying of isolated leaves or branches, from local cross currents which are imperceptible in the observer's position. The prevalence in these regions of dried or damaged leaves among green foliage has already been remarked (p. 272).

Table 3 shows the general divisions of active escape. In every species dodging plays a primary role, although some species are much more adept than others. Jumping, so characteristic of

TABLE 2. DIVISIONS OF PROTECTIVE RESEMBLANCE IN ADULTS

	General Inconspicuousness	Lichen-like Coloration	Twig Mimicry	Leaf Mimicry
Mantoida sp.	x (brown)	–	–	–
Liturgousa sp.	–	x (gray-buff)	–	–
Promiopteryx granadensis	x (brown)	–	–	–
Musonia surinama	–	–	x (brown)	–
Catamusonia sp.	–	–	x (green)	–
Thesprotia filum	–	–	x (brown)	–
Angela quinquemaculata	–	–	x (brown)	–
Acontiothespis multicolor	x (greenish)	–	–	–
Tithrone roseipennis	x (green)	–	–	–
Acanthops falcata	–	–	–	x (brown)
Parastagmatoptera vitrepennis	x (greenish)	–	–	–
Stagmomantis carolina	x (green to brown)	–	–	–
Stagmatoptera septentrionalis	x (green)	–	–	–
Oxyopsis rubicunda	x (male, greenish)	–	–	x (female, green)
Vates lobata	x (greenish)	–	–	–

Table 3. Divisions of Active Escape in Adults

	Retreat	Advance	Dodging; Jumping; Dropping	Fluttering Down	Flight Up
Mantoida sp.	—	—	x	x	x
Liturgousa sp.	—	—	x	x (rare)	—
Promiopteryx granadensis	—	x	x	x	x (rare)
*Musonia surinama**	—	—	x	—	—
Catamusonia sp.	—	—	x	—	—
Thesprotia filum	—	x	x	—	x
*Angela quinquemaculata**	—	x	x	—	x
Acontiothespis multicolor	—	x	x	—	x
Tithrone roseipennis	—	x	x	x	—
Acanthops falcata	x (rare)	x	x	x	—
Parastagmatoptera vitrepennis	—	—	x	—	—
Stagmomantis carolina	—	—	x	—	x
Stagmatoptera septentrionalis	—	x	x	x	x
*Oxyopsis rubicunda**	—	—	x	—	—
*Vates lobata**	—	—	x	—	—

* Observations incomplete.

Note: *Acanthops* alone in the adult sometimes practices kataplexy, which may be considered a subdivision of escape.

most young, varies enormously in the adult; in *Promiopteryx* it is important, while in large, heavy females, such as *Stagmomantis* and *Oxyopsis,* and in awkwardly-shaped elongate forms, especially *Thesprotia,* it is practically non-existent.

Dodging is usually followed by dropping, the latter often but not always aided by fluttering in winged forms. True, strong, upward and spiralling flight is confined to *Mantoida* and to a few strong-winged males, notably *Stagmatoptera.* Except in *Mantoida,* however, the strong-flying mantids often drop without using the wings at all. That is not to say, of course, that males of all species cannot fly adequately, since they are obliged to do so in seeking the female; it is merely that most do not depend on their wings as an important means of escape.

Occasionally some species run straight toward the threat, following the break of an immobile period, and climb on it; only one, an *Acanthops,* has ever run directly away when in the adult stage. On each occasion of running toward the threat the mantis has evidently been alert to it, as shown by its previous immobility, with the head turned toward the threat, and by the tilting or movement of the antennae in the fashion of the species when disturbed. It seems clear that this running toward is not an accidental action, nor the casual result of some mantid equivalent of anxiety or fright; rather, it appears to be a definite, adaptive type of defense. Needless to say, the swift method of approach is quite different from the slow stalking and swift final pounce of the mantis on its prey. The adaptive advantage seems certain: it is obviously much more difficult for an animal without bifocal vision, such as a lizard, to back up, change its aim and seize a small mantis which is approaching rapidly, than to catch one which is retreating and can be followed. When the insect actually jumps or climbs on the attacker's head, seizing is practically impossible by a snake or lizard and is difficult even for a nimble-handed monkey.

Mention should be made here of the flash effect in the wingspread of certain species when, after freezing or dodging, they flutter to the ground. In *Tithrone* especially, which was noticed on several occasions in the field, the sudden flash of red wings, followed by green immobility, was exceedingly effective in confusing three independent human observers.

Finally, a particular form of escape, the use of kataplexy, is found in only one genus, *Acanthops,* and then apparently only in occasional females and young. An additional exception was a single young *Thesprotia.*

In Table 4 is shown the specific distribution of the various motions of display. It will be seen that display is most complex in *Stagmomantis,*

TABLE 4. ELEMENTS OF STARTLE DISPLAY

	Antennae Forward	Antennae Back	Mouthparts Open	Forelegs to Sides	Forelegs Up	Forelegs Flexed, Twisted	Prothorax Up	Tegmina and Wings up	Wings Vibrated	Abdomen Up	Abdomen Twitched Up and Down	Abdomen Twisted to Side and Tilted	Side-to-side Swaying	Side-to-side Sidling
Mantoida sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Liturgousa sp.	—	—	—	—	—	—	x	—	—	—	—	—	—	—
Promiopteryx granadensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Musonia surinama	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Catamusonia sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Thesprotia filum	—	—	—	—	—	—	x	—	—	x	—	—	—	—
Angela quinquemaculata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Acontiothespis multicolor	—	—	—	x	—	—	x	x	—	—	—	—	x	—
Tithrone roseipennis	—	—	x	x	—	—	x	x	—	—	x or	x	x	—
Acanthops falcata	x	—	—	x	—	—	x	x	—	x	—	x	x	x
Parastagmatoptera vitrepennis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Stagmomantis carolina	—	x	—	x	—	x	x	x	x	x	x	—	x	x
Stagmatoptera septentrionalis	—	x	—	x	—	x	x	x	x	—	—	x	x	x
Oxyopsis rubicunda	—	x	x	x	—	—	x	x	—	—	x	x	x	x
Vates lobata	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Stagmatoptera and *Oxyopsis,* and only slightly less so in *Acanthops.* Red and/or yellow coloration of wings, abdomen or both are found in all species with four or more elements of display, namely, *Acontiothespis, Tithrone, Acanthops, Stagmomantis, Stagmatoptera* and *Oxyopsis;* no such coloration is found in any of the other species, except to a slight extent in *Angela.* Striking black spots on the forelegs, presented during display and before striking, are found in *Stagmatoptera* and in some specimens of the non-displaying *Promiopteryx;* strong black femoral bars are present in both sexes of *Parastagmatoptera,* although display has not yet been studied in this rare form. A black sternal bar, very evident in the display of green females, is present only in *Stagmomantis.*

The paired black or black and white tegminal spots, sometimes called stigma, which are so characteristic of many mantids the world over, can be detected in *Acanthops, Mantoida, Catamusonia* male, *Acontiothespis, Parastagmatoptera* (female only), *Stagmomantis, Stagmatoptera, Oxyopsis* (female only), and *Vates* (female only). However, even when the spots are fairly well developed, as in female *Stagmomantis* and male *Stagmatoptera,* they are not always conspicuous, if indeed they are visible, in display. In the present group they are really strikingly developed, ocellus-like and clearly to be seen in display only in female *Stagmatoptera,* which we know from Venezuela but have not observed in Trinidad. Even traces of tegminary spots are absent from the following: *Liturgousa, Promiopteryx, Musonia, Thesprotia, Angela, Tithrone* male, *Vates* male and *Parastagmatoptera* male.

B. Young

The first instar was observed in seven of the fifteen species, namely, *Liturgousa, Promiopteryx, Thesprotia, Acontiothespis, Tithrone, Acanthops* and *Stagmomantis.* In these very young mantids, awareness by the mantid of threat is practically never apparent to the observer unless the insect is actually prodded; then it resorts to the simpler forms of escape. Among the various species the behavior of some individual *Stagmomantis* is the most advanced, while *Thesprotia* appears the most unalert and helpless. Direct, backward retreat, almost non-existent in adults, often occurs, whereas purposeful running toward and on the threat is not found before the middle instars. As might be expected, jumping as a means of escape is much more prevalent than in the heavier adults and is clearly correlated structurally with the relatively longer legs (See Beebe, Crane & Hughes-Schrader, 1952, Text–fig. 1). Dodging, that universal ingredient of mantid defense, is present from the beginning but it is not nearly as skillful as in adults; in *Promiopteryx* and *Liturgousa*, however, it is better than the average. There is no evidence that improvement in dodging is the result of learning; rather, it seems to improve suddenly, after the molt to the second instar. Dropping is sometimes present in the very young but in general they are better clingers than the adults and do not have this form of escape developed. Flight is of course physically impossible except in winged adults.

In the first instar there is no period of immobility in response to threat, except in an occasional *Stagmomantis* and in extremely rare individual *Acanthops*. A semi-stick position is assumed in rest by first-instar *Thesprotia* but it does not become complete, or a response to disturbance, until the second; brief, sporadic, semi-stick positions occur in rare individuals of *Acanthops* even in the first instar, both during simple rest and in response to threat; however, they are usually accompanied by some swaying, which in fact appears to be a behavior trait characteristic of all mantids throughout life. The trembling so characteristic of *Acanthops* is present practically from emergence. *Musonia* and *Catamusonia* are unfortunately unknown in the early instars; however, half-grown specimens sometimes assume imperfect stick positions as well-formed as those of the adult. It is interesting that in all of these young except the ant-like first instar *Tithrone* and *Acontiothespis*, the quality of protective resemblance is represented only in a generalized inconspicuousness; the perfect mimicry of leaves and sticks, in both appearance and behavior, comes later.

In all the very young known except *Tithrone*, immobility in response to threat appears suddenly in most individuals in the second instar; in *Tithrone* it is never found before the third, or even later; this may be connected with its "restless," apparently "highly strung" organization, as shown by its swift motions and active antennae, which heightens, at least to human eyes, the ant-like resemblance.

Startle display, even in rudimentary form, does not appear until late, usually in the pre-adult; since that stage is wingless, it cannot of course be complete, but consists merely of high rearing, exaggerated swaying and an up-tilted abdomen which is sometimes pulsed up and down (*Oxyopsis*); rarely (*Acanthops*) the abdomen is slightly tilted laterally, in adumbration of the exaggerated motions. The forelegs are never extended, however, even in *Stagmomantis* in which the black sternal bar is developed several stages before the adult. It must be remembered that rearing, swaying and turned up abdomens are characteristic of rest and/or exploring positions in early instars of most species, even in forms such as *Liturgousa* which never develop a startle display. More will be said of this under the section on the evolution of defense behavior.

Striking at a threat was induced only in rare *Stagmomantis*. In this genus it can be elicited more easily with each instar; pre-pre-adult specimens, although they do not display the sternal band, will strike hard, the forelegs drawn in and the inner surface of the femora rotated forward as in the adult position. A single young *Acanthops* was induced to strike; it was in the pre-adult instar. *Thesprotia* and *Oxyopsis* did not strike before the adult. The behavior of young *Stagmatoptera*, the remaining striker, is unknown.

V. Releasing Mechanisms of Defensive Behavior

A great deal of patient experimental work remains to be done before a clear picture emerges of the releasing mechanisms of mantid defense. However, a few basic conclusions are apparently valid and are presented here. Other aspects have been scarcely touched; their current status will also be summarized, as possible guides for further study. Unless otherwise stated, the genera used in the experiments were the common ones, where plenty of comparison material was available. They included *Liturgousa, Promiopteryx, Thesprotia, Stagmatoptera* and *Stagmomantis*, supplemented by restricted observations on the rarer forms.

Effect of Physiological State.—The defensive behavior of mantids, in contrast to sexually motivated behavior in animals generally, is apparently not activated by internal factors. The insect must at all times be ready to respond adequately to potentially threatening external stimuli. There is no place here for appetitive behavior, nor, it seems, except perhaps in rudimentary fashion, for hierarchical organization characteristic of certain complex sexual patterns, such as in the three-spined stickleback (Tinbergen, 1950, and ref.) or even in salticid spiders (Crane, 1949). A mantid does not *necessarily* pass through the following very common sequence: awareness of threat . . . immobility . . . display-when-threat-has-approached-closely-and-escape-is-difficult . . dodging . . . dropping. It may instead display at once, or it may never display at all. Successive blocks obviously do not have to be removed, and the various possible patterns are not mutually exclusive, nor must they be used if at all in a certain order. For example, freezing may come last, on the ground, after the insect has dropped or fluttered. Or freezing may both precede and follow the whole sequence, with or without display in the middle.

Similarly, unlike display in sexually motivated animals, there seems to be no individual physiological rhythm even in their startle displays, striking or general pugnacity. As might be expected, a lack of alertness and energy, and a disposition to simple retreat rather than effective freezing, dodging, flying, displaying or fighting, is evident in mantids which are aged or injured or weak from heat, cold or desiccation. The only effect of hunger, except in actually weakened specimens, appears to be that these mantids treat as prey insects which are larger than those they usually seize. There is unquestionably a great amount of individual variation within a species in the tendency to special defense behavior, especially in display and striking. Sexual dimorphism in defense behavior has not yet been sufficiently investigated for comment, nor have the effects of possible territoriality.

No accumulation of display behavior is apparent. Reared mantids which have never been exposed to a normal threat, such as a lizard, nor used in experiment situations, are seemingly no more and no less likely to display, or to display more or less vigorously or completely, than wild or reared individuals which have been used in repeated experiments over a period of days. As with any type of behavior, however, defensive behavior becomes exhausted rather quickly during a single experimental session. This applies particularly to flight and display elements.

Role of Eyes and Antennae in Defense Behavior.—Experiments to determine the role of these organs were conducted in *Liturgousa, Promiopteryx, Thesprotia* and *Stagmatoptera.* Opaque black paint was used to blacken the compound eyes and ocelli. The antennae were amputated at the distal end of the enlarged basal segment. Since anaesthesia was not needed for either operation, its possible effects did not need to be taken into account. No signs of shock were apparent in the subsequent behavior of the insects, although in order to allow for them no tests were made on the day of the operation. The following results were obtained:

1. Neither compound eyes nor ocelli are necessary to release defensive behavior characteristic of the species, including stickmaking in *Thesprotia* and display in *Stagmatoptera.* Surprisingly, when all four visual organs are blackened, display in *Stagmatoptera* is released rather more easily – by a *natural* threat such as a lizard – and continues for a longer time, probably because no new visual stimuli appear to supersede the old; the display is, however, poorly directed and, unlike its usual behavior, the insect does not tend to fly. Blinded *Thesprotia,* when in stick position, will turn its head in accordance with the progress of a moving finger or lizard almost or completely with the precision of normal individuals. Striking and biting on contact are unimpaired in the various genera and display can be intensified by touch. However, completely visual stimuli, such as a long pencil manipulated gently and without vibration of the perch, or apparently air, do not release defense behavior in any of the genera.

2. The antennae are not necessary to release complete and normal defensive behavior in either sex of otherwise normal *Liturgousa, Thesprotia* or in male *Stagmatoptera* (the female not being available for testing). However, *Promiopteryx* of both sexes were more affected; with suitably sized *Gonotodes* as a threat they did not freeze or otherwise behave as normal adults, acting instead like first instar young. The exploring motions of the forelegs were made by *Promiopteryx* about as frequently as in normal individuals.

The exaggerated quivering or lowering of the antennae in normal *Tithrone, Acontiothespis* and *Acanthops* in the presence of snakes and lizards, indicates that some kind of chemical sensations are probably involved. However, no mantid has ever been induced to show any evidence of awareness to odor only, as when placed on the freshly vacated perch of a lizard in its long-occupied terrarium.

3. When compound eyes are blackened and antennae cut off, great differences are apparent in the behavior of all the species tested. There is practically no movement of any kind unless the insect is actually touched. At that time, it moves off slightly and then once more becomes motionless, or rarely drops clumsily to the ground. The only self-impelled motions are slight and include rare swaying and grooming motions on the eyes; there is no turning of the head toward a disturbance, no stiffened freezing, stick-making, display, dodging or flight.

Tactile stimuli, including probing from the front and pinching, are often important in releasing striking and biting behavior; in fact, almost any individual mantid will make biting motions if seized and held, whether or not striking is part of its defense behavior pattern. These tactile stimuli in combination with visual stimuli sometimes induce display where vision alone does not.

Shaking of perches (the observer being concealed) does not produce defense behavior. The first response is merely a tighter clinging to the branch, followed eventually by a rather leisurely shift of position. Only the most violent shaking results in dropping or flying, and then usually only in the smaller mantids.

In no mantids did the simple tapping of its dorsal surface induce display or any part of display (such as wing elevation). This is in contrast to the "reflex" behavior described by Chopard for old-world Orthoptera (1939, p. 365 ff.).

There is no evidence that any sense equivalent to *hearing* plays a part in releasing defense behavior in the Trinidad species.

Since display is often most easily induced in a more or less enclosed space, some sort of *kinaesthetic* sense may be involved. Possibly, however, the effect is due only to the visually perceived proximity of surrounding objects.

Freezing is a response only to a threat at a distance, whether perceived through the eyes or the antennae; it does not occur to a threat very close by or to contact.

Sudden motion is more effective than gradual in inducing display.

The *effective distance* at which the various types of defense behavior occur varies with the species, the size of the threat and the threshold of excitement in the mantid. As a very general rule, however, in small and moderate-sized mantids awareness of threat, as indicated by watching and freezing, occurs at six or eight inches; escape behavior and display, from four inches to contact.

The *size* of an object treated as a threat has definite limits, depending on the size of the mantid. In general, any nearby moving object larger than the mantid but not larger than about ten times its own length (exclusive of long, slender tails) will be treated as a threat. Smaller objects are usually treated as prey and larger ones ignored. Borderline objects, such as katydids or grasshoppers of similar or shorter length but greater bulk than the mantid, may be subjected to display and attack but are usually not treated as prey. When a mantid freezes or displays before a human being, the insect directs the display toward the moving hand, not toward either the observer as a whole or to his face. Similarly, a *Thesprotia* in stick formation beside a passing lizard turns its head in accordance with the changing location of the reptile's *head.* (Pl. II.) However, a *Stagmatoptera* or *Stagmomantis* displays to a monkey as a whole.

The *color* of a threatening object does not appear to be of importance.

The *shape* of an object, so long as it is not a simple geometrical form, may range through wide extremes. Stimuli ranging from a slender dissecting needle to a monkey have been used successfully, each in at least two species. Squares, circles and parallelograms or their three-dimensional counterparts have never attracted any attention at all, no matter how rapidly or erratically they were manipulated.

A puzzling fact is that, while a number of highly artificial "threats" were successful, no model of a living threat has ever drawn defense behavior. The artificial ones included needles, forceps, variously colored sticks and pencils, all manipulated from a distance by black-taped tongs and with the observer hidden. The unsuccessful models of living threats have included rubber spiders, jointed wooden snakes, plasticine lizards variously painted and a rubber monkey. All were of suitable sizes and manipulated as realistically as possible. The failure throughout is probably because no way has yet been found to move them effectively.

In order to produce sudden motion a small jack-in-the-box was used, again without success. It may be that in this case the model's motion was too brief to serve as a releaser.

A *mirror* placed in front of a mantid will sometimes attract its attention, but only for a few moments, and has not yet released defense behavior.

In summary, it is already clear that the releasing mechanisms for defense behavior in mantids are widely and usefully tolerant. They are adapted to respond at need to the enormous variety of motions, sizes, shapes, colors and chemical stimuli which proceed from the hosts of animals which are the natural predators of mantids. Also, appropriate behavior responds promptly to a partial or very imperfect stimulus configuration. Finally, no part of defense behavior depends for its release on only one or two narrow, specific signals.

Nevertheless, the defense behavior patterns of mantids are not perfect. Often appropriate behavior is not released by natural enemies, and the mantid is eaten. (Plate III). Some elements should probably be regarded as displacement activities or merely the results of the simultaneous activation of antagonistic drives. Some of these seem clearly to have been only partly or not at all ritualized, and are certainly not fully evolved elements in adaptive defense. These points will be discussed in the following section.

VI. Evolutionary Aspects

A. Escape and Immobility

As has been shown in preceding sections, immobility and active escape are universally distributed defense behavior mechanisms in mantids. Display and striking, on the other hand, occur in only a few groups and in these rather unpredictably and in serious emergencies only. The same basic dependence on the first two is characteristic of probably the majority of free-living animals, while defensive displays and physical attacks are relatively rare: there are many more rabbits, of whatever phylum, in the world than rattlesnakes, and the usual first lines of defense in even the deadliest snakes are still immobility and escape.

Certainly these two first lines are the oldest in the world; since even amoebae have avoiding reactions, perhaps escape may be termed the oldest of all. It will be recalled that in almost all first instar mantids, active escape is the primary line, while in older mantids stillness comes first. Whether or not this is of phylogenetic significance is open to question: first instar mantids are always more mobile than any instar with the exception of adult males. The "restlessness" of the first instar is doubtless correlated with their need of prompt dispersal, both for increasing their food supply and for discouraging cannibalism. Although first instar young have periods of normal quiet, the daily hours of immobility characteristic of adults come later. In these youngest mantids it is perhaps in simple conformity with their high activity that the secondary stillness in response to threat is so rare. An even more important point is that first instar mantids do not show awareness of a threat until it is extremely close; immobility is most effective at a distance, when there is less chance of the predator's having already seen the mantid.

An interesting point to keep in mind is that in mantids immobility is also the usual first phase in the stalking of prey. Possibly this preface to the specialized stalking sequence evolved originally from the ancient defense element. Even now some stimuli within a certain range of characteristics are treated as potential food as soon as their size or behavior or other traits release hunting rather than defense elements in the mantid.

B. Protective Resemblance

The importance of background resemblance in mantid defense has already been stressed. As Cott says (1940, p. 347), "Compared with stillness cryptic coloration is relatively unimportant, but combined with stillness it is all important." In mantids a wide range of adaptive radiation is shown. In the most generalized form, well illustrated in Trinidad by *Liturgousa, Promiopteryx* and *Tithrone,* the quiet insect tones in exceedingly well with a dark background or one in which brown or green predominates, respectively. However, none would be conspicuous on any usual form of vegetation. In more specialized genera, special resemblance is found to parts of the background, namely sticks and leaves.

The stick-making forms are confined, in the Trinidad genera, to *Musonia, Catamusonia, Thesprotia* and *Angela,* a group of undoubtedly related mantids from whatever viewpoint the phylogeny of mantids is pursued. All have an elongate form, while the first tibia is more or less reduced, and all except *Angela* have completely wingless females. Display was never induced in any of them, except briefly for several elements in one female *Thesprotia* and the single male *Angela.* In these four Trinidad stick makers the general position in stick formation is the same, although the perfection of it and the readiness to adopt the stick position show some variation. In each of them the forelegs are extended to the front, closely apposed, while the head and antennae are tilted back, so that the line of the forelegs is unbroken with that of the prothorax; the abdomen is usually also straightened rigidly, though it may be curved up. The whole insect is often flattened against the substratum by means of the wide lateral extension of the second and third legs.

The origin of the stick-formation is perhaps shown in the peculiar, jerking, exploratory reaches of *Promiopteryx,* which is considered by most authorities (e.g., Chopard) to be part of the same major group as the stick-makers. Somewhat similar jerks or extensions are shown by the young *Liturgousa* when stalking prey and young *Thesprotia, Acontiothespis* and *Tithrone* when exploring, all of which belong to entirely separate groups. From the behavior alone it appears likely that sensory impressions in all of these are being received through the first legs; however, there is absolutely no experimental or structural support yet for this hypothesis, which remains quite untested. An extremely interesting point is that a moderately complete stick position is assumed in *Acanthops,* a relative of *Acontiothespis* and *Tithrone* rather than of the stick-makers, but only in certain young individuals; this is always only as part of the motionless response to threat — that is, in response to the same signals which bring on full stick-position in the regular stick-mantids.

Outside of the mantids, stick-making appears sporadically in other insects, notably in the heteropteran *Emesa* (Pl. IX, Fig. 42) and in the phasmids. The comparison of Trinidad stick-mantids with phasmid sticks from the same locality is interesting. There are two common local representatives, a giant walking-stick (a phibalosominine probably of the old genus *Bacteria* according to Rehn; Pl. IX, Fig. 41) and a much smaller species. In both, the stick form is even more exaggerated than in the mantids: the long antennae are laid forward in a groove formed by the apposition of the extended forelegs, where they are quite concealed. In the smaller species even the second and third pairs of legs are laid forward and back, respectively, parallel and close to the body, and the entire insect becomes rigid, in full kataplexy. Unlike the mantids it does not turn its head in accordance with the progress of the threat or change its position by imperceptible degrees or swift dodging. The mantid, although less specialized for its role of stick-mimic, has preserved the advantage of adaptive behavior.

Examples of the parallel development of stick mimicry in other groups are given by Cott with excellent illustrations of a grasshopper, a caterpillar and a bittern (1940, pp. 334-336; 378-379). In addition, Chopard (1938, p. 409) mentions especially the non-phasmid orthopteran *Parasosibia.* Stick formation in these latter forms is, from the accounts, apparently a normal rest position. In the Trinidad phasmids the signal seems to be tactile or the result of shaking rather than primarily visual as in the mantids; however, this has not yet been sufficiently investigated. Stick formation does not, any more than in the local mantids, appear to be the usual rest position of the phasmids.

Specialized leaf mimicry, as distinct from simple green or brown coloration (as in *Tithrone* or *Promiopteryx*), is confined in the local mantids to five genera belonging to two principal groups. The first, *Acanthops,* the best of the dead-leaf mimics, is a member of the old subfamily Hymenopodinae and is among those with the primitive chromosome pattern. The remaining leaf-mimics are confined to the old Mantinae-Vatinae assemblage and have the advanced chromosome pattern. They include the females of *Parastagmatoptera, Stagmomantis, Stagmatoptera,* and *Oxyopsis;* of these the latter is the most perfect, while the resemblance is little marked in *Vates.* All of these are more or less faithful imitations of green, fresh leaves. It is interesting that mimicry reaches its height in the sedentary females in which the power of flight is greatly reduced; in the males the mimicry has made only slight headway against the necessary functional efficiency of the tegmina and wings, which remain almost as toughly membranous as in the primitive *Mantoida.* Another related genus, known from the adjacent mainland, *Choeradodus,* is the extreme of perfection in green-leaf mimicry, even the pronotum being laterally expanded and aiding in the resemblance.

Comments on the leaf-in-a-breeze-like behavior of *Acanthops* have already been made (p. 272). In origin it is almost certainly a direct modification of the universal mantid habits of swaying and teetering, to be discussed a little later in connection with display. It has been reported also in a Guiana mantid (Hingston, 1932, p. 276) and in old-world forms. (See Chopard's comment, 1938, p. 424).

Cryptic resemblance to general environment and specialized mimicry of sticks and leaves are basically closely related. In both types the result is to make the animal inconspicuous through resemblance to the immediate environment, or to particular, adjacent vegetable objects, all of which are ignored by predators. The majority of the few experimental studies performed on mantids indicate that in this group as in others, protective resemblance has a definite survival value (see survey and references in Cott, 1940, pp. 179-181). The value of special coloration in making the mantid inconspicuous (or, possibly, attractive) to its prey also should not be forgotten. (See especially the well-known cases of apparent floral simulation; comments pro and con, and references, are given in Cott, 1940, p. 49; Chopard, 1938, pp. 420 and 423; and Varley, 1939, p. 92 ff.).

The other major type of resemblance, the defensive mimicry of particular animals which are to be avoided, is practically non-existent in mantids. The local exceptions are the first instars of the related genera, *Tithrone* and *Acontiothespis.* Both of these, in appearance and activity, are astonishingly similar, to human eyes, to small black and red-headed ants, respectively (p. 270, Pl. X, Figs. 43-45). Similar likenesses in this group of genera have already been remarked by Rehn (1935, p. 252).

Bequaert (1922, 1930) has given a large body of evidence showing that ants have many kinds of enemies, and reasons that they are therefore not particularly suitable models for the protection of more defenseless insects. However, as Cott remarks (1940, pp. 167 ff.), it is *relative* immunity from *some* enemies that is conferred on ants by their aggressiveness, stings and unpalatability. And again (Tinbergen, 1950, p. 343): "Primarily we know animals that have developed structures, colour markings or behavior patterns that prevent the situations which would release feeding activities from stimulating the predator. We possess a great many descriptions of, at least from the point of view of *our* sense organs, protective structures, protective colour markings or protective attitudes. It is a pity that we possess only a few experiments to show sceptics that these developments really mean a protection, not towards all enemies and in all cases, but towards those enemies that use for finding their prey the sense organs to which the protective organs correspond, and in the statistical majority of cases. The kataplexy of a beetle when attacked will not protect it from being stung by a beetle-hunting digger wasp, but it may save it from animals like many reptiles that only snap at a prey when it moves."

We have preliminary evidence in Trinidad in support of this view, and in connection with the immediate question. Local small ants of several kinds are similar in appearance to the young *Tithrone* and *Acontiothespis;* they are always disregarded as food by those of our laboratory animals which eat first instar mantids with relish, namely small lizards (*Gonotodes* spp.), yellow-throated frogs (*Prostherapis trinitatis*), other genera of mantids, carnivorous grasshoppers and salticid spiders. We have observed *Gonotodes* in terraria on three occasions for half-hour periods each. During the first session the lizard watched but failed to catch any of a dozen first instar *Tithrone* released near him in a group. A few minutes after they were removed the lizard readily ate several greenish first instar *Stagmomantis;* immediately after that he ate a single young *Tithrone* which was reintroduced. When the group of *Tithrone* was reintroduced it was again disregarded, although a subsequent single one was once more accepted. The same experiment was repeated with similar results on two other *Gonotodes.* Therefore it seems that under natural conditions the resemblance of the swarming, just-hatched mantids to small ants would have a definite survival value; after the mantids have dispersed the resemblance would be far less useful, and in fact it has not been retained in the later instars.

C. Display

The display of mantids is remarkable in a number of ways. First, a conspicuous display in which virtually all the external parts of an animal enter is relatively rare in the animal kingdom. Second, display in mantids is an example of almost purely a bluffing display; against most predators a follow-up by the feeble mantid strike would have little effect; also, it is not a warning against distasteful or injurious qualities in the mantid itself. Third, the origin of the separate elements of mantid display appear to be various, and all, in their evolution, illustrate exceedingly well the operation of the principle of least effort, multiple function being typical of the various parts. Again, although displacement behavior is certainly involved, with or without ritualization, a major factor in its origin seems unquestionably to be the incompatibility of the two simultaneously aroused drives of freezing and flight. Fourth, groups of genera in which mantid display is found are relatively restricted, but include groups which are apparently widely separated phylogenetically. These various aspects will now be developed in more detail.

In completeness of transformation and in the precise correlation of structure and function, a fully displaying mantid ranks with the best in the world. It gives no quarter even to birds-of-paradise, argus pheasants or salticid spiders. In comparison the displays even of fiddler crabs, butterflies, tree frogs and oropendulas are simple and monotonous. However, as in all these animals, the simple general effect of the display is to make the mantid appear larger in size and quite unlike its usual self in its shifting shape and bright color.

All of the non-mantine displays mentioned above are unquestionably connected with the sexual cycle. They are performed either before females, between or among rival males, or are part of the pattern of territorial defense. When any of them displays to an unsuitable object — as when albatrosses, herons or storks perform before men, or peacocks before stones — each case is of course merely an example of a low threshold response to a partial stimulus situation. When mantids display, however, it appears to be altogether non-sexual in function, even though it is at its optimum only in vigorous adults. It never occurs between similar-sized males, although one of these may kill and eat the other at the first opportunity. Similarly, it is not a part of courtship. On only two occasions have I seen even a trace of it. One was when a male *Stagmomantis* was courting an unreceptive female; she displayed very briefly in fending him off. Similar behavior was seen in a pair of *Tithrone* which had already mated and were being kept temporarily in very confined quarters without food. The next morning early both were displaying and attacking each other. Display was never a part of normal courtship. Since no territorial behavior has yet been discovered in mantids (although it may very likely exist, especially in some large, sedentary females such as *Stagmomantis*), display for territorial defense is unknown. In *Liturgousa, Promiopteryx* and *Tithrone,* all of which are somewhat gregarious, it apparently does not exist at all, but of these three only *Tithrone* displays. Finally, no display is ever made to prospective prey, which is always stalked with the utmost inconspicuousness.

For comparison with equally non-sexual displays of "intimidation," two good examples are a sphingid caterpillar, *Leucorhampha,* and the Frilled Lizard, *Chlamydosaurus.* Both are illustrated in Cott, 1940, pp. 215 and 218.

In mantid display, as has been said, the displaying insect as usual seems larger, brighter and very different from its normal self; motion is usually an important factor. The effectiveness of the behavior seems most often to be due not to true intimidation but simply to the momentary respite gained when the attacking predator, such as lizard or monkey, pauses at the sudden apparition — startled, at most, but scarcely truly warned off or "afraid." This gives the insect an opportunity to slip out of the way or fly to safety.

In regard to the effectiveness, to the survival value, of mantid display, only this can be said with certainty: in test situations both in confined terraria, in the open laboratory and in the relative freedom of the large insect house, more than forty separate displays of six species have been performed before lizards, snakes and monkeys. In not one of these cases was the insect ever snapped at, much less eaten, although the same or different individuals a few minutes later, when not displaying, were eaten readily in sixteen cases. Also, one *Stagmatoptera* left in the monkey's cage deterred the monkey during its first two displays but was subsequently eaten in spite of a third. This is in conformity with Carpenter's observations on *Idolum diabolicum* in Africa (1921). It seems that display in the wild must have definite survival value. However, its general unpredictability and the rarity of its occurrence may indicate either its limited usefulness or its recent origin or more probably both.

The evolution of the various elements of startle display is a topic of the greatest interest, although discussion can only be based on speculation. However, the following derivations seem likely for the reasons given in each case. There is obviously, in accordance with the principles of least effort and multiple function (Zipf, 1949), a primary dependence in the evolution of display on the adaptation of structures and behavior patterns originally used for other ends. These have apparently been brought into display through partial or complete ritualization of traits belonging primarily to antagonistic elements of the escape pattern; other important elements are seemingly still of a purely displacement nature, from preying, feeding, sexual grooming, exploring and even resting patterns. Pertinent recent discussions of displacement behavior in general will be found in Armstrong, 1950, and Tinbergen, 1952.

The elevation of the tegmina and wings in display is certainly the most striking single characteristic and, evolutionarily speaking, appears to be the fundamental one. It is probably derived straight from incipient flight and almost certainly arose as a conflict between the impulses to freeze and to fly. That is, it is a typical example of ambivalent behavior as discussed by Tinbergen (1952). Plate IV, Fig. 19, shows a speedlamp photograph of a *Tithrone* in flight; the similarity of the position to that of a displaying mantid is obvious.

Cott (1940, p. 379) suggests reasonably that display in some Orthoptera, particularly grasshoppers, probably developed via the route of flash coloration, bright wing colors being developed first; these deceived the eye on the whereabouts of the insect when it had landed and folded the colors promptly out of sight. Then, as females in particular developed heavy bodies and reduced wings, it became gradually transformed into the relatively sessile performance of an intimidating display. It is certain that, except for the display-prone male *Stagmatoptera*, in Trinidad mantinines it is the females in which both color and readiness to display are most highly developed. In the other displaying group (consisting of *Acontiothespis, Tithrone* and *Acanthops*), the first two show no sexual dimorphism in either color or readiness to display; in both it is induced with difficulty but is complete and effective once it is initiated. In *Acanthops* there is once more strong sexual dimorphism, the male being both duller and less ready to display. Of all the present-day Trinidad mantids, however, whatever their evolution, only *Tithrone* has both the habits and color which make, to human eyes, for effective flash coloration. In all the mantinines, the wings, though often colored, are too dull to give a flash effect in fluttering or in flight. The sporadic and usually ineffectual occurrence of the tegminal stigma has already been discussed. All in all, in Trinidad mantids, there seems to be no reason to attribute the origin of display to flash coloration; the frequently occurring conflict between the freeze and flying drives seems to fit the species much better.

With this hypothesis as a basis the other elements of display appear as mere embellishments, brought into display and in usually intensified form from other behavior patterns.

The elevation of the prothorax, an ever-present element in display, is a mantid habit found to at least a limited extent in all genera studied and at all ages. It is obviously correlated with an outstanding mantid characteristic, their dependence on vision, the range of which is extended periscope fashion by elevation of the eyes. The exaggerated rearing in display, aiding the impression of increased size, seems to be a ritualized outgrowth of this very common action; probably the display origin was a displacement movement during the conflict between freezing and flight. It is interesting that it occurs under similar conditions in both *Liturgousa* and *Thesprotia* which do not have a startle display.

The violent swaying of the prothorax from side to side, so characteristic of advanced displays, can be traced in most species, whether they display or not, back to the first instar. It is almost certainly, in its origins, an aid to vision, particularly in gauging a jump or in the exact location of prey for seizure. Observations of completely undisturbed young mantids will bear this out. In other parts of the animal kingdom similar motions for similar purposes are found in animals with fixed or nearly fixed eyes, such as snakes and most birds (Walls, 1942, p. 307). Here again, the motion in display is probably a ritualized displacement movement, originally connected with the freeze-flight conflict.

The clevation of the abdomen also is found in ordinary rest and locomotion in many very young mantids and in wingless adult females, although in the winged adults of both sexes it is naturally suppressed except when the clevation of the wings makes it possible. In view of the usual resting position of mantids, most of which hang by preference to the underside of stems and twigs, it may originally have been a simple response to gravity, the non-rigid abdomen tending naturally to bend backward. As in displaying species, it occurs sometimes in non-displaying *Thesprotia* before threat, whether or not they are in stick position. It is not visible from the front in the simple erect position and it seems likely that it is an example of non-ritualized displacement behavior.

The twisting, pulsating and tilting of the abdomen, however, is found only in displaying adults in which the abdomen is strikingly colored or at least glossily shining, and it is always very apparent from the front. It seems to have an apparent basis in other activities, although it is possible its origin is as a displaced bit of the sexual pattern. Only the merest foreshadowing is ever seen even in the pre-adult.

The lateral extension of the forelegs, sometimes correlated with black spots or bars, belongs in the general group of size-increasing gestures. The position occurs, in defiance of the laws of stream-lining, in various flying insects with long forelegs, including *Tithrone* (Pl. IV. Fig. 19) and the cerambycid beetle *Acrocinus.*

Teetering on the legs and the general trembling of the body is likewise a universal characteristic of walking mantids and is found also in walking-stick-like phasmids. Following perhaps a sort of principle of uncertainty, it may serve to make mantids less conspicuous in motion; its role in leaf mimicry has already been discussed (p. 278); however, in the exaggerated form it takes in display it certainly makes the insect's appearance more striking. Probably, once again, it is a ritualized form of displacement, this time from the pattern of ordinary locomotion.

Often exaggerated teetering and swaying take place *after* a display followed by an escape, or when the threat, following a freezing position, has passed harmlessly by. Grooming is another frequent activity at this time. It seems that all of these activities are then referable to completely unritualized displacement behavior, the defense pattern energy liberated by the threat stimulus not being yet exhausted.

A final but most effective display detail is found especially in *Oxyopsis* where the mouthparts are both strikingly colored and moved ostentatiously during display. The origin of this certainly must lie in the feeding patterns.

D. Striking

There is little to be said concerning this final, relatively simple element in defensive behavior. It occurs rather rarely, as a concomitant of or instead of display. Sometimes it occurs in young, non-displaying mantids. When associated by *Stagmatoptera* with display, it has resulted in lizards, monkeys and katydids turning around and retreating rapidly. Once a large *Polychrus* was literally knocked halfway off his branch, so that he hung head downwards, by the force of a *Stagmatoptera* blow. After regaining his balance he promptly turned tail and retreated. In none of these attacks does an attempt appear to be made to seize the threat, as in the case of prey. Instead both forelegs are thrust out, unflexed, from the tightly flexed position; then after a raking motion of the tibial teeth they are swiftly returned again to position.

A very widespread and ancient urge exists in the animal kingdom to struggle, bite, kick or otherwise protest physically against seizure, with any available structural equipment; it is a truism that the latter is often specially adapted to serve these ends. Nevertheless, it seems likely that the derivation of the striking motion and its correlated armature in mantids lies wholly in the prey-seizing pattern. After all, non-predatory Orthoptera such as cockroaches and herbivorous grasshoppers do not as a rule strike at their enemies with their forelegs. And it is certainly highly unlikely that the prey-seizing equipment and behavior of mantids evolved from occasional ancestral strikes at contemporary predators.

Biting in mantids occurs only as a last resort, when the insect is seized or teased about the head. It has not been seen to occur in the face of a natural threat.

E. Defensive Behavior and Phylogeny

(For mantid systematic arrangements and discussions see Giglio-Tos, 1927; Rehn, 1935; Beier, 1934, 1937.1, 1937.2; Chopard, 1949; Hughes-Schrader, 1950.)

While the existing systematic arrangements of mantids are in an unsettled state, the general positions allocated to many groups of genera are satisfactory enough. This is true whether mantids as a whole are viewed as divided into the numerous subfamilies of earlier writers or whether Chopard's divisions into a few groups of family rank are accepted.

Defensive behavior substantiates their accepted status. Thus *Mantoida, Liturgousa* and *Promiopteryx* all show unspecialized mantid defense behavior, in agreement with their relatively primitive – though not closely related – positions in structural systematics. By every criterion *Mantoida* is the least specialized. The stick-making forms – *Musonia, Catamusonia, Thesprotia* and *Angela* – comprise, along with *Promiopteryx,* a group of natural affinities, usually divided by systematists among several adjacent subfamilies and apparently all included in Chopard's Thespidae. Display is confined to two specialized groups apparently widely divergent in ancestry, the first having the primitive XO chromosome pattern and the second principally the specialized X^1X^2Y type. They consist, first, of *Acontiothespis, Tithrone* and *Acanthops,* from a single or adjacent subfamilies and regarded as members of Chopard's Hymenopodidae, and, second, of *Parastagmatoptera, Stagmomantis, Stagmatoptera, Oxyopsis* and *Vates,* referred to the Mantidae (in the restricted sense of Chopard) and the Vatidae. The former family has recently been growing at the expense of the latter, and the mixed chromosome patterns indicate that the Vatidae are still a heterogeneous group.

The display behavior of these two unrelated, divergent major groups of mantids – Hymenopodidae on the one hand and Mantidae-Vatidae on the other – is amazingly similar and equally highly evolved. Unfortunately for this comparative study, a primitive display does not occur in the available material. Although the threshold of display is certainly higher in *Tithrone* than in the others, the performance is as complex and well-integrated as any in the series, once release has been attained.

Two instances occur in which the general behavior of Trinidad mantids does not correspond to a particular designated systematic position. These are *Liturgousa* and *Angela,* which were referred by Beier, 1934, to the Mantinae (Chopard's Mantidae). Neither their general habits nor their defense behavior patterns show any similarity to those of the typical Mantinae, nor to each other, except of course for the wide similarities shared by the entire group. On the behavior basis, at least, it seems desirable that their more usual systematic positions be maintained.

Finally, perhaps the most surprising results of the entire study has been the discovery of the similarity of behavior patterns and their releasers throughout the entire group. While display is a characteristic of some of the most specialized, and was apparently developed independently in two branches, the displaying forms also include in defense the elements common to the remaining genera. Also, although there is some evidence that less specialized genera depend relatively more on stimuli received through the antennae, the general wide range of releasers is similar throughout.

F. Conclusion

A few of the foregoing topics require comment or emphasis in reference to problems still untouched. Defensive behavior is unquestionably innate. There was never any evidence that it was in the least improved by practice or by association with other individuals. Its various parts appear, as has been said, somewhat incompletely and at different points in the life history. Nevertheless, except for dodging, they are either well done at once or not at all. If the first display of a just-molted adult winged *Acanthops,* for example, is fully released, it will be as long and as perfect as one which has been practiced half a dozen times during a month. The first stick formation of a second instar *Thesprotia* – again if fully released – is as perfect as that of an adult. Still to be investigated are the effects on propensity to display of possible territoriality, and of "tameness" induced by prolonged captivity.

The study of display in mantids seems especially rewarding since it is apparently in a less completely evolved stage of evolution than are the precisely functioning sexual displays of birds, salticid spiders, etc. Its releasers are, in conformity with the variety of predators, extremely generalized. From another aspect, there is always uncertainty in the defense responses of mantids, particularly in those forms in which display is developed. One can predict with assurance that a threatened wild turtle will draw in his appendages. Yet a specialized species of mantid remains, after months of fairly intimate observation, largely unpredictable. He may freeze, go off, display or strike, under as nearly similar conditions as can be arranged. Although there are strong probabilities governing the release of three of the responses, the release of display still, after close study, appears erratic and subject to great individual variation in propensity. It seems likely that this uncertainty is largely due to the recent evolution of display, the various elements still partaking somewhat of their probably original displacement function and being as yet only partly ritualized.

The only disappointing aspect of the Trinidad mantids is that no primitive display has yet been found to exist in their behavior patterns. All those so far reported in the literature are also, naturally enough, obviously highly evolved, since they are the ones which are likely to be noticed by biologists in the field who are not conducting special studies on the subject. Perhaps these highly desirable primitive examples will be found among the old-world mantids, possibly among the Empusinae, in which display has been recorded. Their study should make a rewarding contribution to our knowledge of the evolution of animal behavior.

VII. SUMMARY

1. The defensive mechanisms of fifteen species of Trinidad mantids are described and analyzed, including where possible their development during the nymphal stages.

2. They were found to consist of four general types which are, in order of frequency of occurrence: protective resemblance in structure and behavior; active escape; startle display; and active attack.

3. All the fifteen species employ protective resemblance, including associated stillness, and active escape; display is known to occur in six of these and active attack in four.

4. Protective resemblance includes general inconspicuousness combined with stillness; twig mimicry in form, color and attitude; leaf mimicry, similarly attained; and a rare, lichen-like cryptic coloration.

5. The most frequent elements in active escape are dodging, jumping and dropping, which occur in all species; apparent adaptive advance onto the threat, use of wings in fluttering to the ground, and upward flight occur less frequently. Simple running away is usually confined to the very young.

6. Display consists primarily of facing the threat with tegmina and wings raised, while the other parts of the body, especially the forelegs and abdomen, are similarly exhibited. Meanwhile the entire insect sways and sidles in a manner that shows off all the special colors and markings of the presented parts to the best advantage. As usual in display, the effect is to make the insect look larger than, and very diffent from, its ordinary appearance. Altogether, 14 different elements were counted in the various displays. The pattern has definite survival value.

7. Attack is rare and consists of striking with the tibiae of the forelegs. Biting practically never occurs except when the insect is physically seized.

8. First instar mantids rely most on active escape; protective stillness develops later; display and attack are characteristic of adults. In two genera there is a temporary early resemblance, apparently of adaptive value, to small ants.

9. The releasers of defensive behavior, in accordance with the great variety of predators on mantids, are highly generalized. While vision is the most important sense in defense, some defensive behavior can be induced in mantids which are blinded but in which the antennae remain intact.

10. It is suggested that the origins of display probably lie in the ritualization of the simultaneous release of two antagonistic elements of escape — motionlessness and flight — and that the remaining elements were originally displacement activities derived from the fields of ordinary locomotion, rest, feeding, etc.

11. In general, the relationships indicated by the defense behavior patterns agree well with the conclusions drawn previously by students of the group's comparative morphology.

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EXPLANATION OF THE PLATES

Plate I

Fig. 1. *Mantoida* sp. ♂. Rest position. Body length in life, *ca.* 19 mm.

Fig. 2. *Liturgousa* sp. ♂. Rest position photographed in unnatural habitat, to show outlines. Body length in life, *ca.* 24 mm.

Fig. 3. Same. Normal rest position among lichens on tree trunk.

Fig. 4. *Promiopteryx granadensis* ♂. Rest position. Body length in life, *ca.* 17 mm.

Fig. 5. Same, ♀. Rest position. Body length in life, *ca.* 20 mm.

Plate II

Fig. 6. *Catamusonia* sp. ♀. Rest position. Body length in life, 61 mm.

Fig. 7. Same, ♂. Stick position. Body length in life, *ca.* 52 mm.

Fig. 8. *Thesprotia filum* ♀. A common rest position, with partly formed stick attitude. Body length in life, *ca.* 60 mm.

Fig. 9. Same. Complete stick formation. Note backwardly tilted head. The abdomen is sometimes held straight, sometimes, as in this photograph, curved.

Figs. 10, 11, 12. Same, showing progressive turning of head in direction of the head of a passing lizard.

Plate III

Fig. 13. *Acontiothespis multicolor* ♀. In rest position, failing to display before lizard. Body length in life, *ca.* 22 mm.

Fig. 14. Same individual being eaten a few seconds later.

Fig. 15. Same species, but different individual ♀, displaying before lizard.

Fig. 16. Same, showing less extreme display position, the forelegs being flexed.

Plate IV

Fig. 17. *Tithrone roseipennis* ♂. Resting position. Body length in life, *ca.* 23 mm.

Fig. 18. Same, ♀. Body length in life, *ca.* 26 mm.

Fig. 19. Same, in flight to show resemblance of position to basic mantid display posture.

Fig. 20. *Acanthops falcata.* First instar. Resting position. Note similarity to that of adult mantids in general. Body length in life, 7.1 mm. See also Pls. V and X.

Plate V

Fig. 21. *Acanthops falcata.* Pre-adult ♂. Resting position in natural habitat. Body length in life 30 mm.

Fig. 22. Same, ♂. Resting position in natural habitat. Body length in life, *ca.* 39 mm.

Figs. 23, 24. Same. Dorsal and lateral views.

Plate VI

Fig. 25. Same, ♀. Resting position. Body length in life, *ca.* 40 mm.

Figs. 26, 27, 28. Same. Display. See also Text-fig. 1.

Plate VII

Fig. 29. *Stagmomantis carolina* ♂. Rest position. Body length in life, *ca.* 60 mm.

Fig. 30. *Stagmatoptera septentrionalis* ♀. Rest position. Body length in life, *ca.* 75 mm. See also Text-fig. 2.

Fig. 31. Same. Preliminary display attitude.

Fig. 32. Same. Full display before lizard.

Fig. 33. Same. Partial display before young capuchin monkey.

Fig. 34. Same, ♀. Display in a specimen from Rancho Grande, Aragua, Venezuela.

Plate VIII

Fig. 35. *Oxyopsis rubicunda* ♀. Rearing: the first phase of display. Body length in life, *ca.* 65 mm.

Fig. 36. Same. Second phase, showing rearing combined with extension of forelegs.

Fig. 37. Same. Third phase, in which backwardly directed antennae and elevated tegmina are added to the first two elements.

Fig. 38. Same. Full display; here the bright yellow wings are also raised and the shining surface of the abdomen twisted so as to be visible from the front.

Plate IX

Fig. 39. *Vates lobata,* ♀. Rest position in unlikely habitat, to show foliations on legs. Body length in life, *ca.* 60 mm.

Fig. 40. Same, grooming.

Fig. 41. Giant phasmid (?*Bacteria* sp.) in stick position.

Fig. 42. Heteropteran bug (*Emesa* sp.) in stick position.

Plate X

Sketches of first instars from life, showing ant-like facies and positions.

Fig. 43. *Acontiothespis multicolor,* dorsal view. Body length in life, 5.3 mm.

Fig. 44. Same, lateral view.

Fig. 45. *Tithrone roseipennis,* lateral view. Body length in life, 5.5 mm.

Fig. 46. *Acanthops falcata,* lateral view. Ant resemblance not pronounced. Body length in life, 7.1 mm.